





CONTENTS

PART I (Issued 31 December 2000)

ALLSOPP, P.G.	Revision of the Australian genus <i>Anomalomorpha</i> Arrow (Coleoptera: Scarabaeidae: Dynastinae) with a new species from the Wet Tropics of Queensland	1
BAEHR, M.	Some genera and species of ground beetles new to Australia (Coleoptera: Carabidae)	9
BALLANTYNE, L.A. & LAMBKIN, C.	Lampyridae of Australia (Coleoptera: Lampyridae: Luciolinae: Luciolini)	15
BOUCHARD, P.	<i>Cuemus</i> , a new genus of Tenebrionidae (Coleoptera) from the northern Queensland Wet Tropics.	95
CERMAK, M. & HASENPUSCH, J.W.	Distribution, biology and conservation status of the peppermint stick insect, <i>Megacrania batesii</i> (Kirby) (Phasmatodea: Phasmatidae); in Queensland	101
CRANSTON, P.S.	Three new species of Chironomidae (Diptera) from the Australian Wet Tropics.	107
DAVIES, V.T. & LAMBKIN, C.	<i>Wabua</i> , a new spider genus (Araneae: Amaurobioidea: Kababiniinae) from north Queensland, Australia.	129
GROVE, S.J.	Trunk window trapping: an effective technique for sampling tropical saproxylic beetles	149
HARVEY, M.S.	A review of the Australian schizomid genus <i>Notozomus</i> (Hubbardiidae).	161
HOWDEN, H.F. & STOREY, R.I.	New Stercomerini and Rhyparini from Australia, Borneo and Fiji (Coleoptera: Scarabaeidae: Aphodiinae).	175
KOHOUT, R.J.	A review of the distribution of the <i>Polyrhachis</i> and <i>Echinopla</i> ants of the Queensland Wet Tropics (Hymenoptera: Formicidae: Formicinae).	183
O'KEEFE, S.T. & MONTEITH, G.B.	<i>Clidicus abbotensis</i> O'Keefe, a new species of Scydmaenidae (Coleoptera: Staphylinioidea) from Australia with description of the larva.	211
RAVEN, R.J.	A new species of funnel-web spider (<i>Hadronyche</i> : Hexathelidae: Mygalomorphae) from north Queensland.	225
REID, C.A.M.	A complex of cryptic species in the genus <i>Coptodactyla</i> Burmeister (Coleoptera: Scarabaeidae: Coprini)	231
REID, C.A.M. & STOREY, R.I.	Revision of the dung beetle genus <i>Temnoplectron</i> Westwood (Coleoptera: Scarabaeidae: Scarabacini)	253
SINCLAIR, D.P.	Two new genera of Tessaratomidae (Hemiptera: Heteroptera: Pentatomoidea).	299
SINCLAIR, D.P.	A generic revision of the Oncomerinae (Heteroptera: Pentatomoidea: Tessaratomidae)	307
SLANEY, D.P.	New species of cave dwelling cockroaches in the genus <i>Neotemnopteryx</i> Princis (Blattaria: Blattellidae: Blattellinae).	331
STANISIC, J.	Taxonomy of the Australian rainforest snail, <i>Helix bellendenkerensis</i> Brazier, 1875 (Mollusca: Eupulmonata: Camaenidae).	337
STOREY, R.I. & MONTEITH, G.B.	Five new species of <i>Aptenocanthan</i> Matthews (Coleoptera: Scarabaeidae: Scarabaeinae) from tropical Australia, with notes on distribution	349

CONTENTS (continued)

LAMPRELL, K., STANISIC, J. & CLARKSON, P. Spondylids from the Mediterranean Sea and Atlantic Ocean (Mollusca: Bivalvia: Spondylidae) . . .	611
LAMPRELL, K., STANISIC, J. & CLARKSON, P. Some spondylids from the Pacific Ocean (Mollusca: Bivalvia: Spondylidae)	623
LIMPUS, C.J. A breeding population of the Yellow-bellied sea-snake, <i>Pelamis platurus</i> , in the Gulf of Carpentaria	629
LIMPUS, C.J., DE VILLIERS, D.L., DE VILLIERS, M.A., LIMPUS, D.J. & READ, M.A. The loggerhead turtle, <i>Caretta caretta</i> in Queensland: feeding ecology in warm temperate waters.	631
McGUIGAN, K.L. An addition to the rainbowfish (Melanotaenidae) fauna of North Queensland	647
JOINSON, J.W., RANDALL, J.E. & CHENOWETH, S.F. <i>Diagramma melanacrum</i> , new species of haemulid fish from Indonesia, Borneo and the Philippines with a generic review	657
NORMAN, M.D. New octopus species from Queensland	677
OTTO, J.C. Halacaridae from the Great Barrier Reef lagoon and Coral Sea: <i>Halacarellus</i> and <i>Halacarus</i> (Acarina: Halacaroidae).	691
OTTO, J.C. Halacaridae of the Great Barrier Reef Lagoon and Coral Sea: the <i>Copidognathus ornatus</i> group (Acarina: Prostigmata: Halacaridae).	717
RICHARDS, S.J. A new species of torrent-dwelling frog (Anura: Hylidae: <i>Litoria</i>) from the mountains of Indonesian New Guinea (West Papua)	733
ROWE, C., STANISIC, J., DAVID, B. & LOURANDOS, H. The helicinid land snail <i>Pleuropoma extincta</i> (Odhner, 1917) as an environmental indicator in archaeology	741
LOHMANN, U. & SACHS, S. Observations on the postcranial morphology, ontogeny and palaeobiology of <i>Sclerocephalus</i> <i>haeuseri</i> (Amphibia: Actinodontidae) from the Lower Permian of Southwest Germany . . .	771
TIMMS, B.V. A new species of <i>Calamoecia</i> (Copepoda: Calanoida) from arid Australia, with comments on the calanoid copepods of the Paroo, northwestern Murray-Darling Basin.	783
 NOTES	
HANNAH, D. & THURGATE, N.Y. Range extensions for two poorly known Queensland snakes	400
COVACEVICH, J.A., BUFFETT, A.F., COUPER, P.J. & AMEY, A.P. Herpetological 'foreigners' on Norfolk Island, an external territory of Australia	408
McGROUTHER, M.A. First record of the Large-Tooth Cookie-Cutter Shark <i>Isistius plutodus</i> from Australian waters.	442
PALMER, R.A. Southern range extension for the Delicate Mouse (<i>Pseudomys delicatulus</i>).	460
McGROUTHER, M.A. First record of Elsmann's Whipnose Anglerfish, <i>Gigantactis elsmanni</i> (Lophiiformes: Gigantactinidae), from Australian waters	646
ARANGO, C.P. Sea spiders (Pycnogonida) from the Great Barrier Reef, Australia, feed on fire corals and zoanthids	656

BAEHR, B. & JOCQUÉ, R. Revisions of genera in the <i>Asteron</i> -complex (Araneae: Zodariidae): new genera <i>Pentasteron</i> , <i>Phenasteron</i> , <i>Leptasteron</i> and <i>Subasteron</i>	359
CANNON, L.R.G. & SEWELL, K.B. A review of <i>Temnosewellia</i> (Platyhelminthes) ectosymbionts of <i>Cherax</i> (Crustacea: Parastacidae) in Australia	385
COOK, A.G. & CAMILLERI, N. Additions to the rostroconch fauna of Australia and China	401
DALL, W. Australian species of Aristeidae and Benthescymidae (Penaeoidea: Decapoda)	409
DAVIES, V.E. & LAMBKIN, C. A revision of <i>Procambidgea</i> Forster & Wilton, (Araneae: Amaurobioidea: Stiphidiidae)	443
DETTMANN, M.E. & CLIFFORD, H.T. The fossil record of <i>Elaeocarpus</i> L. fruits	461
EWART, A. Dusk chorusing behaviour in cicadas (Homoptera: Cicadidae) and a mole cricket, Brisbane, Queensland	499
FAUBEL, A. & CAMERON, B. Turbellaria from salt marshes of Coomera River, southeastern Queensland, Australia	511
FRITH, C.B. & FRITH, D.W. Bowerbird (Ptilonorhynchidae) biometrics, with observations on sexual dimorphism and intraspecific variation	521
GUILBERT, E. Western Pacific Tingidae (Heteroptera): new species and new records	543
HALLETT, S.L., ERSEUS, C., O'DONOGHUE, P.J. & LESTER, R.J.G. Parasite fauna of Australian marine oligochaetes	555
HEALY, J.M., LAMPRELL, K. & KEYS, J.L. The 'water-trap' spiny oyster, <i>Spondylus varius</i> Sowerby, 1827 G.B. Sowerby I, 1827 (Mollusca: Bivalvia: Spondylidae) from Australia	577
KOFRON, C.P. & SMITH, R. Status of Estuarine Crocodiles in the populated coast of northeast Queensland	603
LAMPRELL, K., STANISIC, J. & CLARKSON, P. Spondylids from the Mediterranean Sea and Atlantic Ocean (Mollusca: Bivalvia: Spondylidae) ..	611
LAMPRELL, K., STANISIC, J. & CLARKSON, P. Some spondylids from the Pacific Ocean (Mollusca: Bivalvia: Spondylidae)	623
LIMPUS, C.J. A breeding population of the Yellow-bellied sea-snake, <i>Pelamis platurus</i> , in the Gulf of Carpentaria	629
LIMPUS, C.J., DE VILLIERS, D.L., DE VILLIERS, M.A., LIMPUS, D.J. & READ, M.A. The loggerhead turtle, <i>Caretta caretta</i> in Queensland: feeding ecology in warm temperate waters	631
MCGUIGAN, K.L. An addition to the rainbowfish (Melanotaeniidae) fauna of North Queensland	647
JOHNSON, J.W., RANDALL, J.E. & CHENOWETH, S.F. <i>Diagramma melanacrum</i> , new species of haemulid fish from Indonesia, Borneo and the Philippines with a generic review	657
NORMAN, M.D. New octopus species from Queensland	677
OTTO, J.C. Halacaridae from the Great Barrier Reef lagoon and Coral Sea: <i>Halacarellus</i> and <i>Halacarus</i> (Acarina: Halacaroidea)	691
OTTO, J.C. Halacaridae of the Great Barrier Reef Lagoon and Coral Sea: the <i>Copidognathus ornatus</i> group (Acarina: Prostigmata: Halacaridae)	717

RICHARDS, S.J.	
A new species of torrent-dwelling frog (Anura: Hylidae: <i>Litoria</i>) from the mountains of Indonesian New Guinea (West Papua)	733
RÖWE, C., STANISIC, J., DAVID, B. & LOURANDOS, H.	
The helicinid land snail <i>Pleuropoma extincta</i> (Odhner, 1917) as an environmental indicator in archaeology	741
LOHMANN, U. & SACHS, S.	
Observations on the postcranial morphology, ontogeny and palaeobiology of <i>Sclerocephalus haeuseri</i> (Amphibia: Actinodontidae) from the Lower Permian of Southwest Germany . . .	771
TIMMS, B.V.	
A new species of <i>Calamoecia</i> (Copepoda: Calanoida) from arid Australia, with comments on the calanoid copepods of the Paroo, northwestern Murray-Darling Basin.	783
NOTES	
HANNAH, D. & THURGATE, N.Y.	
Range extensions for two poorly known Queensland snakes	400
COVACEVICH, J.A., BUFFETT, A.F., COUPER, P.J. & AMEY, A.P.	
Herpetological 'foreigners' on Norfolk Island, an external territory of Australia	408
McGROUTHER, M.A.	
First record of the Large-Tooth Cookie-Cutter Shark <i>Isistius plutodus</i> from Australian waters.	442
PALMER, R.A.	
Southern range extension for the Delicate Mouse (<i>Pseudomys delicatulus</i>).	460
McGROUTHER, M.A.	
First record of Elsmann's Whipnose Anglerfish, <i>Gigantactis elsmanni</i> (Lophiiformes: Gigantactinidae), from Australian waters	646
ARANGO, C.P.	
Sea spiders (Pycnogonida) from the Great Barrier Reef, Australia, feed on fire corals and zoanthids	656



REVISIONS OF GENERA IN THE *ASTERON*-COMPLEX (ARANEAE: ZODARIIDAE): NEW GENERA *PENTASTERON*, *PHENASTERON*, *LEPTASTERON* AND *SUBASTERON*

BARBARA BAEHR AND RUDY JOCQUÉ

Baehr, B. & Jocqué, R. 2001 06 30: Revisions of genera in the *Asteron*-complex (Araneae: Zodariidae): new genera *Pentasteron*, *Phenasteron*, *Leptasteron* and *Subasteron*. *Memoirs of the Queensland Museum* 46(2): 359-385, Brisbane, ISSN 0079-8835.

Four genera are erected to accommodate 13 new species in the *Asteron*-complex, a large group of Australian Zodariidae. *Pentasteron* is characterised by a cymbial concavity. Its type species is *simplex* (♂ ♀) and it is further represented by *parasimplex* (♂), *intermedium* (♂ ♀), *securifer* (♂ ♀), *oseltans* (♂ ♀), *sordidum* (♂), *storosoides* (♂) and *isobelae* (♂ ♀). *Phenasteron* is created for the type species *longiconductor* (♂) and *machinosum* (♂). *Leptasteron* includes the type species *playconductor* (♂) and *vexillum* (♂). Both the later genera are characterised by a sclerotised basal swelling on the subtegulum and a huge DTA with refolded distal margin. They differ mainly by the structure of the carapace, cymbium and tegulum. *Subasteron* contains only the peculiar type species *daviesae* (♂ ♀) diagnosed by shape of the carapace and of the ♂-abdomen and a prolateral tegular apophysis on the male palp. □ *Araneae, Zodariidae, Asteron*-complex, new genera, Australia.

B. Baehr, Queensland Museum, PO Box 3300, South Brisbane 4101, Australia (e-mail: barbara.b@qm.qld.gov.au); R. Jocqué, Invertebrate Section, Royal Africa Museum, B-3080 Tervuren, Belgium (e-mail: jocque@afriamuseum.be); 15 February 2001.

This is the third contribution to the systematics of spiders belonging to the large *Asteron*-complex (Baehr & Jocqué, 1996). Jocqué & Baehr (2001) and Baehr & Jocqué (2000) revised *Asteron* (Jocqué, 1991), to contain 8 species, and *Pseudasteron*, *Cavasteron* and *Minasteron* were erected with 1, 12 and 3 species, respectively. The present paper describes another 4 genera with 8, 2, 2 and 1 species. Whereas the former genera were fairly easily defined as they exhibit clear autapomorphies, it was much more difficult to unite the species that were placed in the basal groups of the cladogram for the *Asteron*-complex that was presented by Baehr & Jocqué (1996). The original idea was to create *Pentasteron* for the 5 basal groups in the cladogram. It proved, however, that this was impossible due to the lack of synapomorphies for this grouping that would have created a paraphyletic taxon in the absence of *Asteron* s. str. Therefore, we have erected 3 new genera; *Subasteron*, is monotypic whereas *Phenasteron* and *Leptasteron* each contain 2 species united by characters of the male palp and carapace shape.

MATERIAL AND METHODS

Descriptions follow Jocqué & Baehr (1992). Abbreviations: ALE, anterior lateral eyes; AME, anterior median eyes; AS, anterior spinnerets; E, embolus; EA, embolar apophysis; DTA, dorsal tegular apophysis; F, femur; FL, flange; LTA, lateral tegular apophysis; MS, median

spinnerets; MT, metatarsus; MOQ, median eye quadrangle; P, patella; PE, prolateral extension of tegulum; PLE, posterior lateral eyes; PME, posterior median eyes; PS, posterior spinnerets; PTA, prolateral tegular apophysis; T, tibia; VTA, ventral tegular apophysis. Abbreviations of institutions where material was borrowed: AM, Australian Museum, Sydney; KBIN, Koninklijk Belgisch Instituut voor Natuurwetenschappen; QM, Queensland Museum, Brisbane; SAMA, South Australian Museum, Adelaide; VM, Victoria Museum, Melbourne; WAM, Western Australian Museum, Perth; ZSM, Zoologische Staatssammlung Muenchen.

SYSTEMATICS

Pentasteron gen. nov.

TYPE SPECIES, *Pentasteron simplex* sp. nov.

ETYMOLOGY. Greek prefix, *penta* = five; with generic name, *Asteron*; referring to 5 basal groups of *Asteron*-complex (Baehr & Jocqué, 1996). Gender is neuter.

DIAGNOSIS. Member of *Asteron*-complex, with ♂-palp having tibia with a deep retrolateral concavity combined with a pronounced concavity on the base of the cymbium, having tegulum with a broad base traversed by the seminal duct and ending in a typical median apophysis (VTA) with curved tip, usually having embolar apophysis (EA) of variable length.

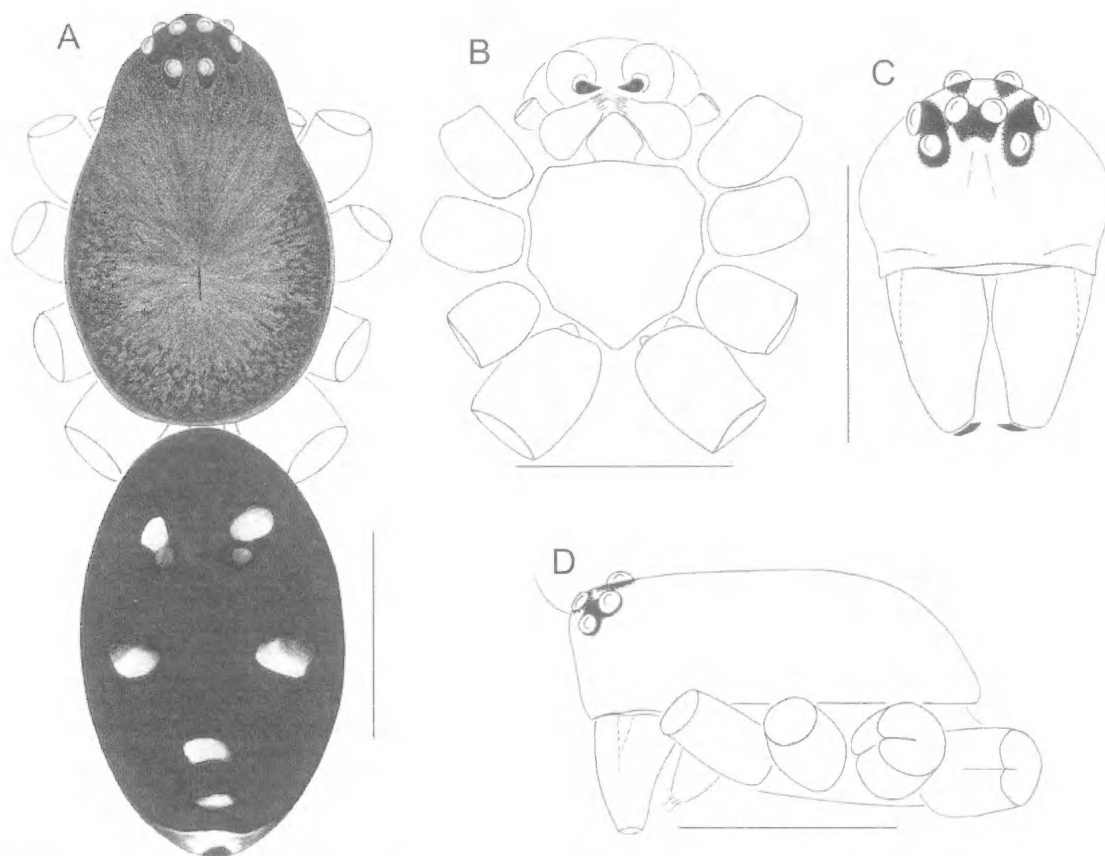


FIG. 1. *Pentasteron simplex*. A, body dorsal; B-D, cephalothorax; B, ventral; C, frontal; D, lateral. Scale 1mm.

DESCRIPTION. Small to medium-sized spiders (3.00-7.00) with slightly granulate tegument. Carapace widest at coxae II, narrowed to 0.60-0.65 maximum width in both sexes. Profile flat with highest point between fovea and PME (Fig. 1A,B).

Colour: carapace dark brown, chelicerae and sternum medium brown; legs with strongly contrasting white to dark brown femora; coxae pale, trochanters dark, other legs yellow or brownish.

Eyes (Fig. 1C, D) in 3 rows (2-4-2). Only ALE in first row, AME (in the middle) and PLE in second, third only PME. Eyes subequal or ALE smaller than rest. MOQ slightly longer than wide. Clypeus straight, about 3 times diameter of ALE; with few hairs. Chilum single, short wide, without setae. Chelicerae as usual for family with a few hairs in front and dense row on distal promargin; no teeth. Labium narrowed at base; sparsely haired. Gnathocoxae rather elongate; sparsely haired; with anteromesal scopula.

Sternum flat; shield-shaped with straight anterior margin and tiny triangular extensions between coxae. No inter- nor precoxal sclerites.

Legs: formula 4123. Spination: few spines on pairs I, II, more numerous on III, IV. Paired tarsal claws with numerous (± 12) teeth on I and II, with ± 7 on III and IV. Unpaired claw toothless, on very small onychium.

Trichobothria in two rows on T, in a single row on Mt and t. Hinged hairs present but few, restricted to dorsal side of TI and II. Metatarsal preening brush on Mt II and III poorly developed.

Abdomen oval; mostly without sigilla but some species with two dorsal and a prolateral one on either side. Spinnerets: AS short, conical, with very short distal segment; MS and PS very short, absent in males. Colulus represented by group of setae. Tracheal spiracle hidden by well developed anterior lip; posterior lip sometimes sclerotised and protruding from under anterior lip.

Male palp (Fig. 2C,D): tibia with large lateral concavity delimited by solid dorsolateral apophysis and ventrolateral apophysis, most often swollen along its lower lateral margin. Cymbium with basal concavity, simple unmodified flange, several spines near distal tip.

Tegulum with broad base carrying transverse section of seminal duct; distal part extended in typical median apophysis (VTA) with curved tip. Embolus emerging on prolateral part of tegulum. Several species with split relatively short, rigid embolus, dorsal prong of variable length. LTA usually short and thorn-like. DTA membranous, simple.

Epigyne: external structure simple, with central depression, sometimes double; copulatory ducts starting near centre or slightly in front, running towards the side and backward to enter simple, thick-walled spermathecae. Female palp with finely dentate claw.

KEY TO THE SPECIES OF *PENTASTERON*

1. Males 2
Females 9
2. Embolus not bifid 3
Embolus bifid (Figs 3E,H, 4C,F,I, prolateral view) . . . 5
3. Tegulum with very large prolateral extension (PE), guiding embolus (Fig. 5A) *P. securifer*
Tegulum without such extension 4
4. Tegulum with large half funnel-shaped VTA (Fig. 5C,D) *P. isobelae*
VTA not half funnel-shaped, but straight (Fig. 3A) *P. parasimplex*
5. Cymbium with very large retro-basal cymbial concavity delimited by triangular flap (Fig. 4B) *P. oscitans*
Cymbium with small concavity (Figs 3D,G, 4E,H) . . . 6
6. EA at base thicker than embolus (Fig. 3H) *P. intermedium*
EA at base not thicker than embolus (Figs 3E, 4F,I) . . . 7
7. EA bifid at distal end; dorsolateral tibial apophysis recurved (Fig. 4D-F) *P. storosoides*
EA not bifid at distal end; dorsolateral tibial apophysis not recurved (Figs 3E, 4I) 8
8. EA longer than embolus, clearly visible in ventral view (Fig. 4G) *P. sordidum*
EA shorter than embolus, not visible in ventral view (Fig. 3C,E) *P. simplex*
9. Central part of epigyne clearly delimited, with inverted v-shaped ridge, or at least rebordered in front (Figs 6E,F, 7A,B) 11
Central part of epigyne poorly delimited, front never rebordered 12
11. Epigyne with inverted u-shaped ridge only in front (Fig. 7A) *P. securifer*
Epigyne with inverted v-shaped ridge for more than half of epigyne (Fig. 6E) *P. intermedium*

12. Posterior margin of epigyne clearly indented (Fig. 6C) *P. oscitans*
Posterior margin sometimes sinuous but not indented (Figs 6A, 7C) 13
13. Posterior margin of epigyne straight (Fig. 7C) *P. isobelae*
Posterior margin of epigyne sinuous (Fig. 6A) *P. simplex*

***Pentasteron simplex* sp. nov.** (Figs 1A-D, 2A-D, 3C-E, 6A,B, 15)

ETYMOLOGY. For the simple genitalia.

MATERIAL. HOLOTYPE: ♂, Lake Broadwater, via Dalby, SE Qld, pitfalls site 1, 13.i-25.ii.1986, QM & M. Bennie (QMS15746). PARATYPES: Queensland: 58 ♂, 6 ♀, together with holotype (QMS52610; 2 ♂ in KBIN; 1 ♂ 1 ♀ in ZSM); 1 ♂, Christmas Creek, xi.1912, E. Mjöberg (RMS). NSW: 1 ♂, Myall Lakes NP, 32°30'S 152°21'E, 14.xii.1996, L. Wilkie (MLCO/05) (AM KS 55653); 1 ♀, Myall Lakes NP, 32°37'S 152°12'E, 14.xi.1996, L. Wilkie (MLIO/03) (AM KS 55654); 1 ♂, as previous; 32°17'S 152°12'E, 15.xii.1996 (MLIO/01) (AM KS55650); 1 ♀, Myall Lakes NP, 32°37'S 152°12'E, 14.xii.1996, L. Wilkie (MLIO/01) (AMKS55651); 1 ♂, 15.xii.1996, further as previous (MLIO/05) (AM KS55652); 3 ♂, Booti Booti NP, 32°16'S 152°31'E, 13.xii.1996, L. Wilkie (BBIO/09) (AMKS55659); 1 ♂, as previous (BBIO/06) (AMKS55644); 1 ♀, as previous, (BBIO/01) (AMKS55645); 1 ♂, as previous (BBIO/05) (AM KS55648); 1 ♀, as previous, 13.xi.1996 (BBIO2/01) (AM KS55647); 2 ♂, as previous (BBIO/09) (AM KS55659); 1 ♀, as previous (BBIO01/09) (AM KS55643); 1 ♀, as previous (BBIO2/09) (AMKS55649); 1 ♂, as previous, 32°14'S 152°32'E, 14.xii.1996, L. Wilkie (BBCO2/07) (AM KS55646); 1 ♀, Munmorah State Rec., 33°13'S 151°34'E, 16.xii.1996, L. Wilkie (MUNIO2/04) (AMKS55655); 1 ♀, Wyrabalong NP, 33°16'S 151°32'E, 16.xii.1996, L. Wilkie (WYRCO02/07) (AM KS55658); 1 ♂, as previous, 16.xi.1996 (WYRCO02/10) (AM KS55657); 1 ♂, as previous, 16.xi.1996 (WYRCO01/09) (AM KS55656); 2 ♂, Ramornie SF, Main Ck, track off Mt. Tindal, 29°43'S 152°38'E, 4.ii-9.iii.1993, M. Gray & G. Cassis (AMKS39135); 1 ♂, Ramornie SF, Mt Tindal, 29°42'S 152°35'E, 4.ii-9.iii.1993, M. Gray & G. Cassis (AMKS 39136); 5 ♂ 1 ♀, Ramornie SF, track off T-Ridge Rd, Mt Tindal, 29°33'S 152°38'E, 4.ii-9.iii.1993, M. Gray & G. Cassis (AMKS39134).

DIAGNOSIS. ♂♂ are recognised by simple palpal organs: dorsolateral tibial apophysis with broad base, split embolus with thin and short EA; ♀ epigyne simple with a longitudinal pale zone in middle; the copulatory openings are at margin of this zone just in front of centre.

DESCRIPTION. *Male* (holotype). Total length 3.56; carapace 1.85 long, 1.22 wide; tibia+patella 1.59.

Colour: Carapace medium brown with darker

radiating striae; chelicerae and sternum reddish brown; coxae pale with dark pro- and retrolateral spots; trochanters dark; proximal half of femora white with dark proximal ring, distal half dark brown; patellae brownish yellow suffused with dark brown on sides and with dark distal ring; tibiae brownish yellow, II, III and IV darkened on ventral and lateral sides. Abdomen dark sepia to black; dorsum with narrow dark brown scutum in front and 7 white spots: 2 pairs in anterior half, 3 in a row in front of spinnerets; sides with large oblique white spot; venter uniform dark sepia with 2 small yellow spots in front of epigastric fold.

Carapace finely granulated; sternum not granulated.

Eyes: a: 0.10; b: 0.10; c: 0.11; d: 0.12; e: 0.02; f: 0.02; g: 0.04; h: 0.08; AL-AL: 0.18. MOQ: AW = 0.84 PW; AW = 0.78 L.

Clypeus 0.32 or 3.2 times ALE. Chilum single, 0.08 high, 0.38 wide.

Spination:

	I	P	T	Mt
I	pl1d2	-	v2	v4
II	pl3d2	-	v2	v5 dw3
II1	pl2d3rl2	pl1d1rl1	pl2d2rl2v1-2-2	10disp dw5
IV	pl2d4rl1	pl1d1rl1	pl2d2rl2v1-2-2	10disp dw5

No hinged hairs.

Male palp (Fig. 3C-E): tibia with large retrolateral concavity delimited by ventrolateral lamellate apophysis with swollen lateral margin and dorsal, short, blunt downpointing apophysis. Cymbium with shallow basal concavity and fairly long flat flange (FL). Embolus short, rigid, curved outward, split at base, EA thin, short, only visible from prolateral side. VTA short, sturdy; DTA membranous, attached to dorsal part of VTA.

Female (paratype). Total length 4.31; carapace 1.98 long, 1.35 wide; tibia+patella I: 1.58.

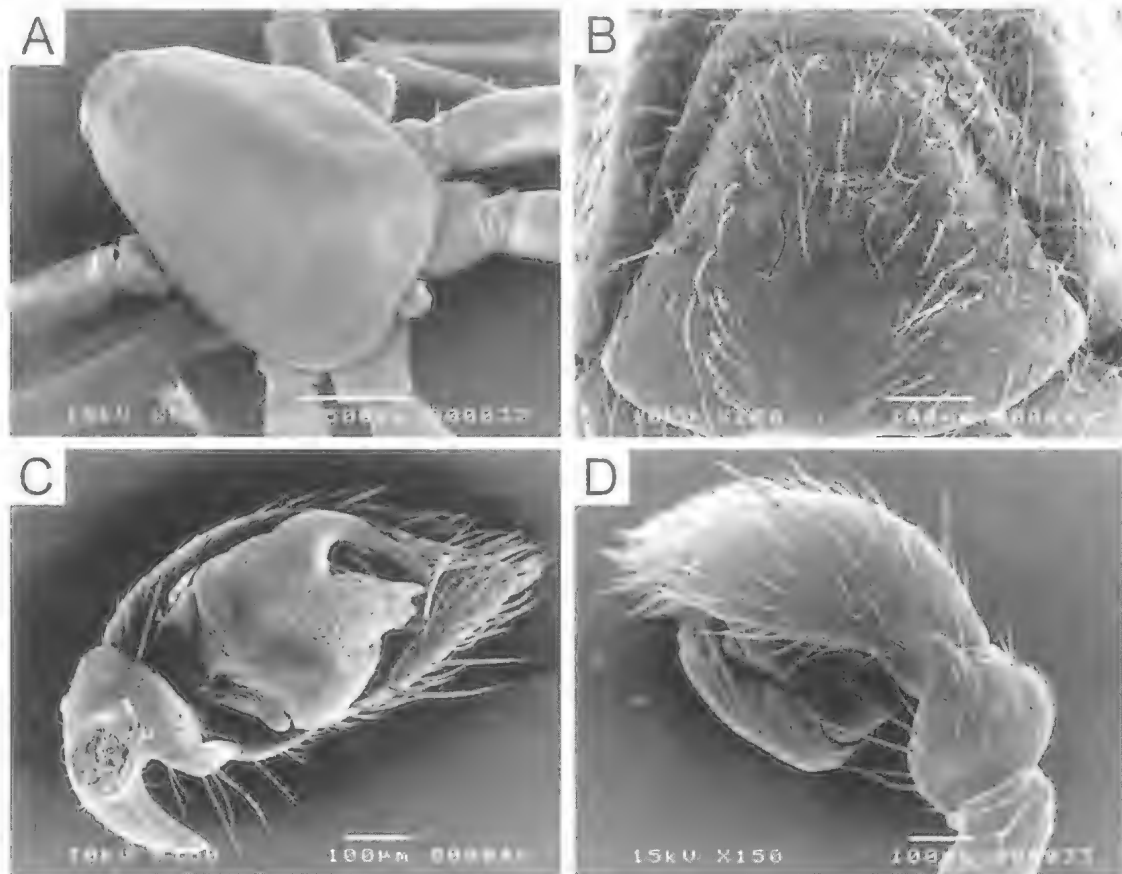


FIG. 2. *Pentasteron simplex*; A, cephalothorax dorsal; B, epigyne; C, D, left male palp; C, ventral; D, retrolateral.

Colour: exactly as in male.

Eyes: a: 0.10; b: 0.10; c: 0.12; d: 0.12; e: 0.04; f: 0.04; g: 0.04; h: 0.10; AL-AL: 0.20. MOQ: AW = 0.86 PW; AW = 0.71 L.

Clypeus 0.34 or 3.4 times ALE. Chilum single, 0.07 high, 0.36 wide

Spination:

	F	P	T	Mt
I	pl1d2	-	v2-2	v2-1-2
II	pl1d2	-	v2-1-2	v4 dw3
III	pl3d3rl1	pl1d1rl1	pl2d2rl2v2-2-2	9disp dw5
IV	pl2d3rl1	pl1d1rl1	pl2d3rl3v2-2-2	9disp dw5

Hinged hairs: TI d1, TII d1.

Epigyne(Fig. 6A,B): very simple: with hardly sclerotised plate with slightly concave posterior rim; copulatory openings in front, fairly closely set under semicircular darker shields; internal structure showing through translucent epigyne. Copulatory ducts very broad at entrance, describing more than one loop before entering small lateral spermathecae.

Variation: colour pattern and size very stable: ♂ carapace length 1.82-1.87 and width 1.20-1.22; ♀ carapace length 1.92-1.98, width 1.33-1.40.

DISTRIBUTION. Known only from type locality.

***Pentasteron parasimplex* sp. nov.**
(Figs 3A,B, 15)

ETYMOLOGY. Similar to *P. simplex*.

MATERIAL. HOLOTYPE: ♂, Wyperfield NP, Victoria, Dattuck track, *Eucalyptus foecunda* leaf litter, 2.vii.1982, M. Harvey & B. Roberts (WAM).

DIAGNOSIS. Coloration very uniform; ♂ ♂ with swollen ventrolateral tibial apophysis and very short LTA.

DESCRIPTION. *Male* (holotype). Total length 4.03; carapace 2.08 long, 1.40 wide; tibia+patella 1.85.

Colour: Carapace, chelicerae and sternum pale brown, patternless; legs uniform yellowish brown; abdomen dark sepia: dorsum with narrow brownish frontal scutum and five pale spots, 2 pairs and single one in front of spinnerets; venter pale sepia.

Carapace and sternum smooth.

Eyes: a: 0.14; b: 0.10; c: 0.12; d: 0.12; e: 0.02; f: 0.04; g: 0.06; h: 0.10; AL-AL: 0.26. MOQ: AW = 1.00 PW; AW = 0.75 L.

Spination:

	F	P	T	Mt
I	pl1d2	-	v2-1-2	v2
II	pl1d2	-	v1-2-1	v4
III	pl3d3rl2	pl1d1rl1	pl2d2rl2v2-2-2	7disp dw6
IV	pl2d4rl1	pl1d1rl1	pl3d3rl3v2-2-2	9disp dw6

Hinged hairs: TI d1, TII d1.

Abdomen with 2 dorsal sigilla and a lateral in front on either side.

Male palp (Fig. 3A,B): tibia with deep retrolateral concavity; ventrolateral apophysis swollen, rounded at the back, blunt in front; dorsolateral one fairly short and thick, sharp, pointing outwards; cymbium with fairly long flat flange, with small proximal indentation; embolus short, rigid, curved outwards; without EA; VTA short, rigid, blunt; DTA membranous; LTA very short with thick base and sharp tip.

Female unknown.

DISTRIBUTION. Known only from type locality.

***Pentasteron intermedium* sp. nov.**
(Figs 3F-H, 6E,F, 15)

ETYMOLOGY. Refers to its intermediate taxonomic position.

MATERIAL. HOLOTYPE: ♂, Augusta, Cave Break road, Western Australia, 34°20'S 115°09'E, *Agonis* & moss litter, 24.vii.980, S. & J. Peck (WAM 90/170-1). PARATYPES: 1 subadult ♂, together with holotype; South Australia: 1 ♂, Blinman, 8-19.xii.1986, post office, on floor, 31°05'S, 138°40'E; M. Dykshoorn (SAMA); 1 ♂, Kolay Hut, 32°33'S 135°36'E, 10.xii.1989, on ground, D. Hirst (SAMA N1992120); New South Wales: 1 ♂, Federal Highway on NSW/ACT border, 35°12'S 149°12'E, 10.v.1992, J. Hunt (AM KS49459); Victoria: 2 ♀ 2 ♂, Barr Ck, Kervins Rd, Cohuna, 35°48'30"S 144°10'30"E, 1 May 1999, watering, J. Hooper, D. & J. Shield, J. Woodman (S30490); 1 ♀, Upper Lurg, 36°35'S, 146°11'E, col. J. Strudwick 14, Jan 1997 (JSt 529); 1 ♂, same data as previous (JSt 550); 1 ♀, same data as previous, 4 Apr 2000 (JSt 717); 1 ♀ 1 ♂, Spring Gully, 36°37'48"S, 144°15'17"E, J. Shield, 22-30 Dec 1993 (CVIC 777); 1 ♀, same data as previous, 18 Jan 1994 (CVIC 790); 2 ♀ 2 ♂, Barr Creek, Cohuna, 35°48.5'S, 144°10.5'E col. J. Hooper, D & J Shield, J. Woodman 1 May 1999, watering (CVIC 785).

DIAGNOSIS. Males have a unique combination of sclerites in the palp: large VTA, small spine-like LTA and large curved EA accompanying embolus along its dorsal side. Female has a simple epigyne with clearly delimited inverted v-shaped ridge in front, pale zone on posterior half.

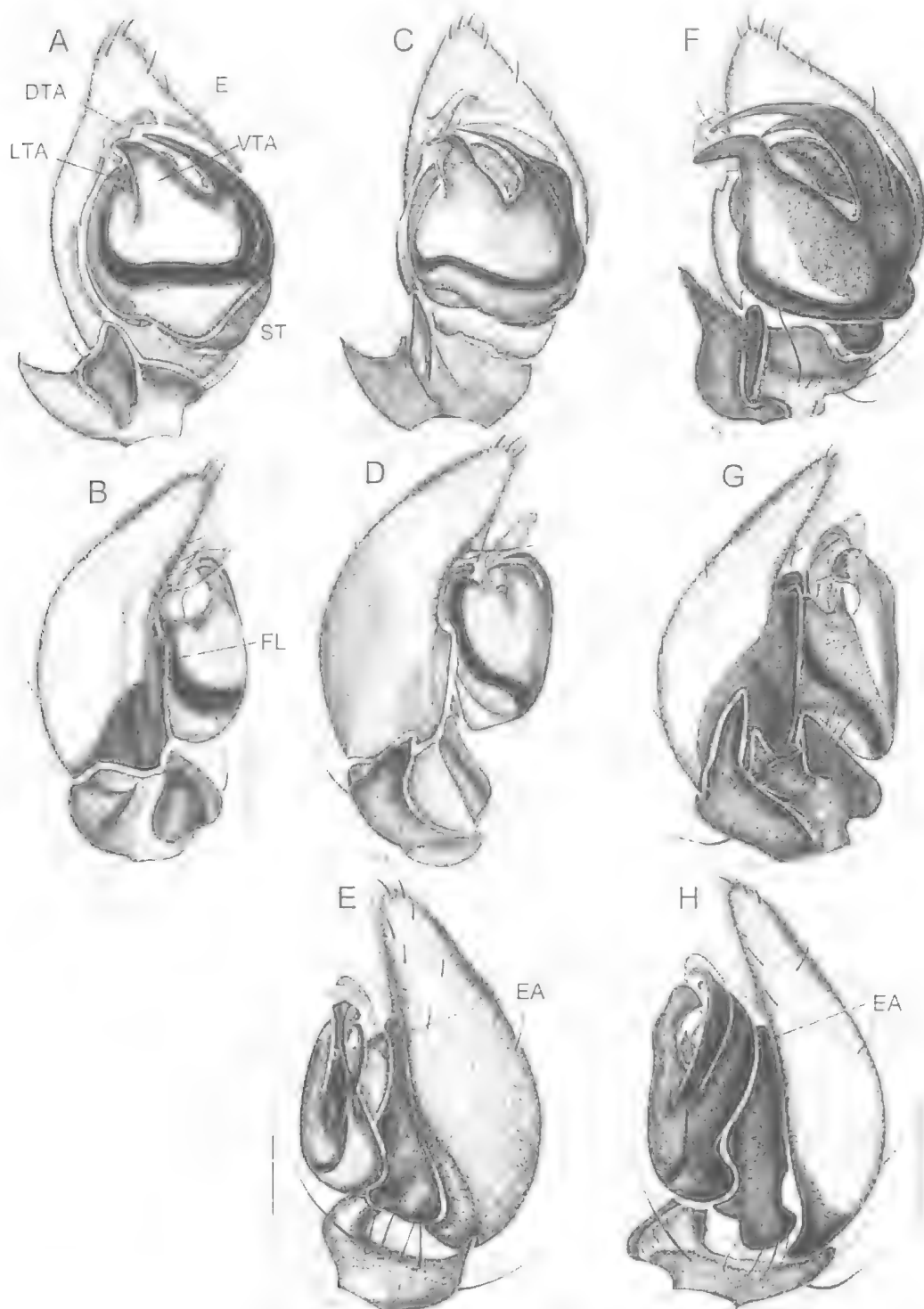


FIG. 3. *Pentasteron* spp. right male palps. A,B, *P. purasimlex*; A, ventral; B, retrolateral; C-E, *P. simplex*; C, ventral; D, retrolateral; E, prolateral; F-H, *P. intermedium*; F, ventral; G, retrolateral; H, prolateral. Scale 0.5mm. DTA = dorsal tegular apophysis, E = embolus, EA = embolar apophysis, LTA = lateral tegular apophysis, ST = subtegulum, VTA = ventral tegular apophysis.

DESCRIPTION. *Male* (holotype). Total length 3.42; carapace 1.72 long, 1.18 wide; tibia+patella I 1.50.

Colour: Carapace medium brown with faint radiating striae and V-shaped dark mark in front of fovea. Chelicerae and sternum medium brown, slightly suffused with black. Coxae pale, trochanters pale brownish yellow suffused with black on sides; femora dark brown with paler dorsal lines, in distal third, pale in proximal part; patellae, tibiae and metatarsi orange brown, tibiae with slightly darkened sides. Abdomen dark sepia to black; dorsum with 4 pale spots in frontal half and 3 pale chevrons, posterior 2 anatomising, in front of spinnerets; sides with oblique pale stripes, venter pale sepia with broad pale median stripe and a spot on either side in front of dark ring around spinnerets.

Carapace very finely reticulated; sternum smooth.

Eyes: a: 0.09; b: 0.10; c: 0.10; d: 0.10; e: 0.02; f: 0.02; g: 0.04; h: 0.08; AL-AL: 0.18. MOQ: AW = 0.83 PW; AW = 0.62 L.

Clypeus: 0.3 or 3.0 times diameter of ALE.

Spination:

	F	P	T	Mt
I	pl1d2	-	v1-1	v2
II	pl1d2	-	v1-1	v2-1dw3
III	pl1d3	pl1d1r1	pl2d2rl2v2-2	8isp dw6
IV	pl2d4	pl1d1r1	pl3d3rl3v2-2-2	8isp dw6

One dorsal hinged hair on tibiae I and II.

Male palp (Fig. 3F-H): tibia with large retrolateral concavity delimited by fairly flat ventrolateral lamellate apophysis with dorsal swelling and roughly triangular (as seen from above) flat dorsolateral apophysis with denticle at its dorsal base. Cymbium with fairly extensive flange. Embolus fairly short and rigid, curved outward, split at base, the dorsal prong (EA) thick and well developed. VTA well developed and strong; DTA membranous, attached to tegulum dorsad of VTA; LTA a short spine-shaped excrescence between sperm-duct and VTA.

Female (paratype). Total length 4.83; carapace 2.08 long, 1.33 wide; tibia+patella I: 1.58.

Carapace medium brown with faint darker radiating striae; chelicerae and sternum medium brown; sternum pale brown; coxae pale, brownish towards base; trochanters brownish yellow suffused with black on sides; femora white with small basolateral ring in proximal half, dark brown in distal half; remainder of legs yellowish brown, tibiae suffused with dark on

sides; abdomen dark: dorsum with 2 pairs of white spots in frontal half and 3 pale chevrons in a row in front of spinnerets; sides with 2 or 3 pale stripes; venter pale sepia with pale median stripe and a spot on either side in front of dark ring around spinnerets. Lung covers yellow.

Eyes: a: 0.10; b: 0.10; c: 0.14; d: 0.12; e: 0.04; f: 0.04; g: 0.04; h: 0.08; AL-AL: 0.18. MOQ: AW = 0.80 PW; AW = 0.66 L. Clypeus 0.36.

Chilum single, 0.08 high, 0.48 wide.

Spination:

	F	P	T	Mt
I	pl1d2	-	v2-2-2	v2
II	pl1d2	-	v1-2-2	v2-2 dw3
III	pl2d3rl2	pl1d1r1	pl2d2rl2v2-2-2	8disp dw6

Hinged hairs: TI d1, TII d1. Preening brush on Mt II and III.

Epigyne (Fig. 6E,F): clearly delimited inverted v-shaped ridge in front, pale zone on posterior half; copulatory ducts showing trough tegument; copulatory ducts large, strongly sclerotised, directed diagonal, ending in poorly delimited, adjacent caudal spermathecae.

Variation: ♂ carapace length: 1.72-1.84, carapace width: 1.18-1.30. Colour of carapace in South Australian specimens darker; leg colour stable; abdomen without spots or with 5 tiny spots; slight variations in shape of palpal sclerites, such as curvature of VTA and EA.

DISTRIBUTION. Western and South Australia.

Pentasteron securifer sp. nov.

(Figs 5A,B, 7A,B, 15)

ETYMOLOGY. Latin: *securis*, an axe, refers to shape of the huge, H-shaped VTA.

MATERIAL. HOLOTYPE: ♂, John Forrest NP, Western Australia, (31°52'S, 116°04'E) 1967, G.H. Lowe (WAM 90/272). **PARATYPES:** 2 ♀, Jarrahdale Mine site, Western Australia, 32°13'S 116°04'E, 12-18.iv.1999, KEG. Brennan (WAM 99/2378-2379).

DIAGNOSIS. ♂♂ have a very typical palp with very large, H-shaped VTA of which retrolateral distal part is axe-shaped; ♀♀ have an epigyne with fairly deep, roughly diamond-shaped central depression, clearly delimited in front.

DESCRIPTION. *Male* (holotype). Total length 4.79; carapace 2.40 long, 1.63 wide; tibia+patella I 2.45.

Colour: Carapace medium brown with faint darker radiating striae and V-shaped pattern in

front of fovea; chelicerae medium brown, paler along median margin; sternum pale brown, slightly darker along margin; coxae pale yellow; trochanters pale brown; femora pale in proximal half, brown in distal half; tibiae I pale yellow, II, III and IV slightly darker slightly suffused with dark on sides; metatarsi and tarsi brownish yellow; abdomen sepia; dorsum with narrow brownish frontal scutum and six pale spots, 1 pair in front, one in the middle, and two in line in front of spinnerets; sides with large oblique pale area; venter pale, darker in front of epigastric furrow.

Carapace and sternum smooth.

Eyes: a: 0.12; b: 0.12; c: 0.14; d: 0.14; e: 0.02; f: 0.04; g: 0.06; h: 0.12; AL-AL: 0.28. MOQ: AW = 0.94 PW: AW = 0.83 L.

Spination:

	I	P	IV	Mt
I	pl1d2	-	v2-2	v1-1-2-2
II	pl1d2	-	v1-1	v1-1-2-2
III	pl3d3r3	pl2r1	pl1d2r2v2-2-2	8disp dw6
IV	pl2r4r1	mt1	p-12v3-	0-1-1-5-6

Hinged hairs: TI d1, TII d1.

Male palp (Fig. 5A,B): tibia with deep retrolateral concavity, delimited by 2 large apophyses; ventrolateral apophysis flat, rebordered along margin, dorsolateral one roughly quadrangular with anterior corner drawn out into short sharp prong; cymbium with flat flange provided with backward directed prong, and with poorly defined distal haired ridge thus forming concavity; embolus long and slender, originating on posterior end of tegulum which has huge, roughly H-shaped VTA; its retrolateral distal prong is broad, axe-shaped and runs subparallel with membranous DTA; retrolateral part broadly connected with prolateral part which accompanies the embolus on its ventral side; LTA tiny spine; without EA.

Female (paratype). Total length 4.36; carapace 2.40 long, 1.62 wide; tibia+patella I: 2.06.

Carapace dark brown with faint darker radiating striae; chelicerae and sternum medium brown; sternum pale brown; coxae pale, yellowish towards base; trochanters dark with pale yellow ventral patch; femora white with small basolateral spots in proximal half, dark brown in distal half; remainder of legs yellowish brown, tibiae suffused with dark on sides; abdomen dark; dorsum with 6 white spots, 1 pair in front, 1 in the middle, and 2 in a row in front of spinnerets; sides with large oblique spot; venter fairly pale, paler centrally; lung covers yellow.

Eyes: a: 0.10; b: 0.10; c: 0.11; d: 0.12; e: 0.03; f: 0.03; g: 0.05; h: 0.08; AL-AL: 0.19. MOQ: AW = 0.86 PW: AW = 0.76 L. Clypeus 0.32.

Chilum single, 0.06 high, 0.22 wide.

Spination

	I	P	IV	Mt
I	pl1d2	-	v2-2-2	v2
II	pl1d2	-	v1-2-2	v2-2 dw3
III	pl3d2r2	pl1d1r1	pl2d2r2v2-2-2	8disp dw3

Hinged hairs: TI d1, TII d1. Preening brush on Mt II and III.

Epigyne (Fig. 7A,B): with fairly deep, roughly diamond-shaped central depression, deeper in front, there delimited by posteriorly indented plate; copulatory ducts clearly showing trough tegument; copulatory ducts large, strongly sclerotised, ending in poorly delimited, adjacent, caudal spermathecae.

DISTRIBUTION. Known only from type locality.

***Pentasteron oscitans* sp. nov.**
(Figs 4A-C, 6C,D, 15)

ETYMOLOGY. Latin *oscitare*, accommodating; refers to the shape of the male palpal cymbium.

MATERIAL. HOLOTYPE: ♂, Barrington Tops State Forest, 1.4 km S along Bungaree trail from Barrington Tops Forest Rd, NSW, 31°56'S 151°21'E, 4.ii-9.iv.1993, 1180m (NPWS survey), M. Gray & G. Cassis (AM KS039485). PARATYPE: 1 ♀, together with holotype.

DIAGNOSIS. ♂♂ have a very large cymbial fold; ♀♀ differ in the shape of the posterior indentation of the epigyne.

DESCRIPTION. *Male* (holotype). Length 3.56; carapace 1.85 long, 1.22 wide; tibia+patella I 1.59.

Colour: Carapace chestnut brown; chelicerae medium brown; sternum medium brown with yellow posterior tip; coxae white with dark brown rim; trochanters dark with yellow ventral patch; femora white in proximal half, dark brown in distal half; patellae yellow with darker distal section; tibiae with white proximal part preceded by thin dark ring and dark distal part; metatarsi and tarsi yellowish brown. Abdomen shiny black; dorsum with two pairs of small white spots, sides with one oblique white spot; venter sepia, slightly paler in front of epigastric fold.

Carapace finely granulated; sternum smooth.

Eyes: a: 0.10; b: 0.10; c: 0.11; d: 0.12; e: 0.02; f: 0.02; g: 0.04; h: 0.08; AL-AL: 0.18. MOQ: AW =

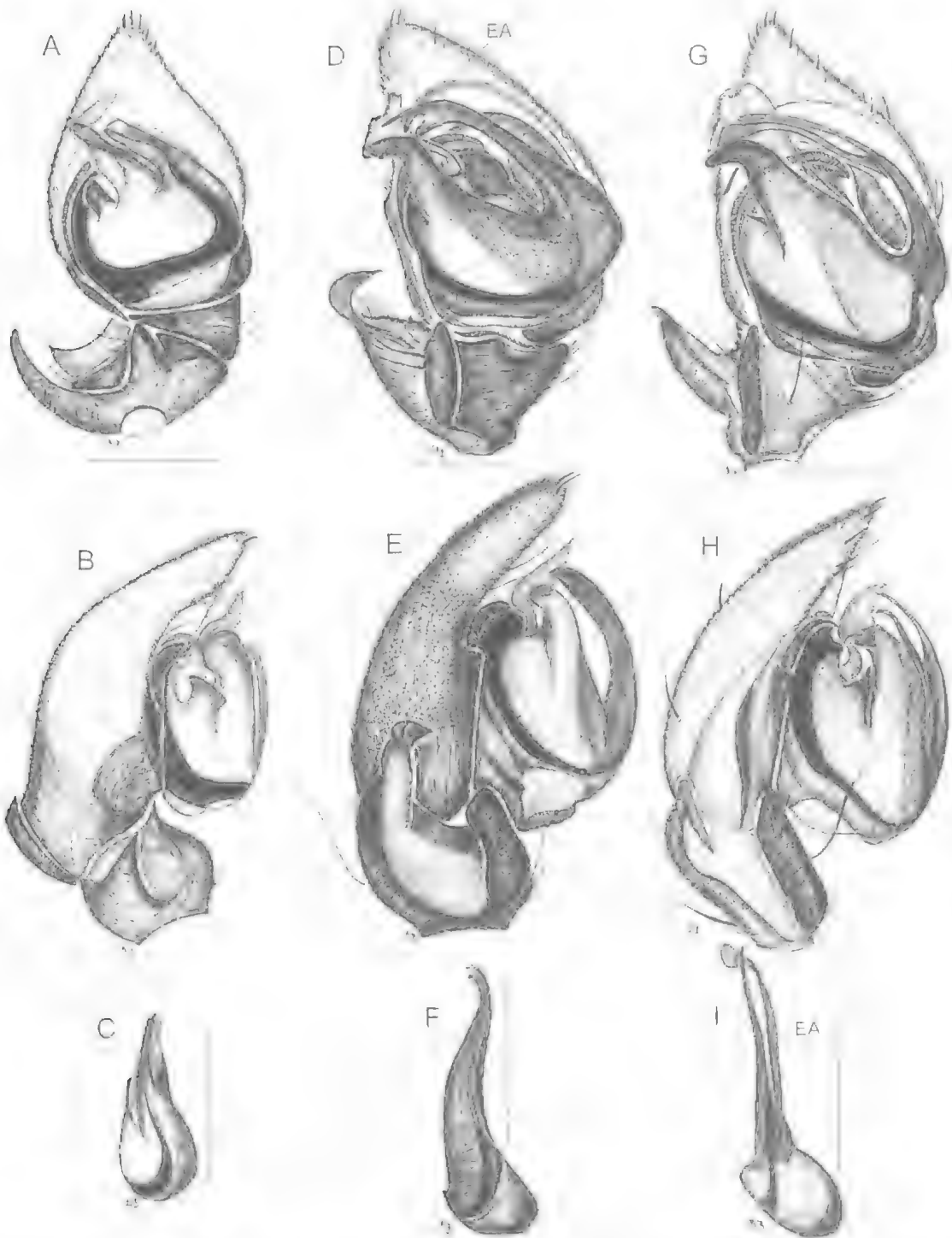


FIG. 4. *Pentastemon* spp. right male palps. A-C, *P. oscitans*; A, ventral; B, retrolateral, C, embolus with embolar apophysis, prolateral. D-F, *P. storosoides*; D, ventral; E, retrolateral; F, embolus with embolar apophysis, prolateral. G-I, *P. sordidum*; G, ventral; H, retrolateral; I, embolus with embolar apophysis, prolateral. Scale 0.5mm.

0.84 PW; AW = 0.78 L. Clypeus 0.30. Chilum 0.03 high, 0.13 wide.

Spination:

	F	P	T	Mt
I	d2	-	v2	v2
II	d2	-	v2	v2
III	pl3d3rl3	pl1d1rl1	pl2d2rl2v1-2-2	8disp dw5
IV	pl3d3rl2	pl1d1rl1	pl2d3rl2v1-2-2	10disp dw5

Hinged hairs: TI and TII: d1. Preening brush on Mt II and III.

Abdomen with large rounded lip in front of tracheal spiracle. Colulus with 3 setae.

Male palp (Fig. 4A-C): tibia with large retrolateral concavity delimited by elongate, roughly triangular, pointed dorsal apophysis and ventrolateral lamellate apophysis. Cymbium with large proximal fold, forming concavity together with tibial concavity, dorsally delimited by large triangular flap; cymbial flange unmodified. Tegulum broad based, tapered toward rounded VTA; LTA short, truncated, broader at extremity than at base; DTA membranous, distally sharply curved outwards. Embolus short, thick, rigid, curved outward; with thin short EA.

Female (paratype). Total length 4.31; carapace 1.98 long, 1.35 wide; tibia+patella I: 1.58.

Colour: As ♂ but sternum uniform medium brown. Palp: femora dark brown with pale ventral patch, other segments yellow.

Eyes: a: 0.10; b: 0.10; c: 0.11; d: 0.12; e: 0.03; f: 0.03; g: 0.05; h: 0.08; AL-AL: 0.19. MOQ: AW = 0.86 PW; AW = 0.76 L. Clypeus 0.32.

Chilum single, 0.06 high, 0.22 wide.

Spination:

	F	P	T	Mt
I	d1	-	v2-2-2	v2
II	d1	-	v2-1-2	v2
III	pl2d3rl1	pl1d1rl1	pl2d2rl2v2-2-2	8disp dw5
IV	pl2d3	pl1d1rl1	pl2d2rl2v2-2-2	10disp dw5

Hinged hairs: TI d1, TII d1. Preening brush on Mt II and III.

Epigyne (Fig. 6C,D): simple, sclerotised plate with 2 depressions (entrance openings) centrally; posterior clearly indented. Copulatory ducts and spermathecae strongly sclerotised.

DISTRIBUTION. Known only from type locality.

***Pentasteron sordidum* sp. nov.**
(Figs 4G-I, 15)

ETYMOLOGY. The name refers to the colour of the male which is rather 'dirty' (Latin: *sordidus*).

MATERIAL. HOLOTYPE: ♂, Lake Wytchugga, 6km w. Wilcannia, New South Wales, 21-22.xii.1998, M. Baehr (QM S46889).

DIAGNOSIS. ♂♂ have a palp with deep tibial concavity delimited by the large longitudinal swollen ventrolateral swelling and a ventrally ridged dorsolateral apophysis.

DESCRIPTION. *Male* (holotype). Total length 4.88; carapace 2.38 long, 1.56 wide; tibia+patella I 1.74.

Colour: Carapace chestnut brown; chelicerae and sternum medium brown; coxae pale; trochanters yellowish brown; femora I yellowish brown with darker patches at base and tip; femora II-IV white in proximal half, yellow overlaid with dark brown in distal half; other parts yellow. Abdomen grey mottled with white and black, yellowish in front of epigastric fold and on lip in front of tracheal spiracle.

Carapace finely granulated; sternum smooth.

Eyes: a: 0.15; b: 0.14; c: 0.14; d: 0.14; e: 0.03; f: 0.02; g: 0.04; h: 0.10; AL-AL: 0.26. MOQ: AW = 1.03 PW; AW = 0.87 L. Clypeus 0.42 or 3.0 times ALE. Chilum 0.08 high, 0.30 wide.

Spination:

	F	P	T	Mt
I	pl1d2	-	v2-2-2	v1-1-1-1
II	d2	-	v2-2-2	v1-1-1-1dw3
III	pl3d3rl2	pl1d1rl1	pl2d2rl2v2-2-2	8disp dw5
IV	pl2d3rl1	pl1d1rl1	pl3d3rl3v2-2-2	lost

Hinged hairs: TI and TII: d1. Preening brush on Mt II and III.

Abdomen with large rounded lip in front of tracheal spiracle. Colulus a group of c. 10 setae.

Male palp (Fig. 4G-I): tibia with large retrolateral concavity delimited by thick longitudinal ventrolateral swelling and large dorsolateral, ventrally ridged apophysis; cymbium with basal fold linked up with tibial concavity. Tegulum broad at base, tapered toward strong VTA which has tip curved outward; LTA short, thorn-shaped; DTA membranous, widened toward broadly truncate extremity. Embolus fairly short, curved outward, thin but rigid; with EA longer than embolus proper, slightly widened at tip.

Female unknown.

DISTRIBUTION. Known only from type locality.

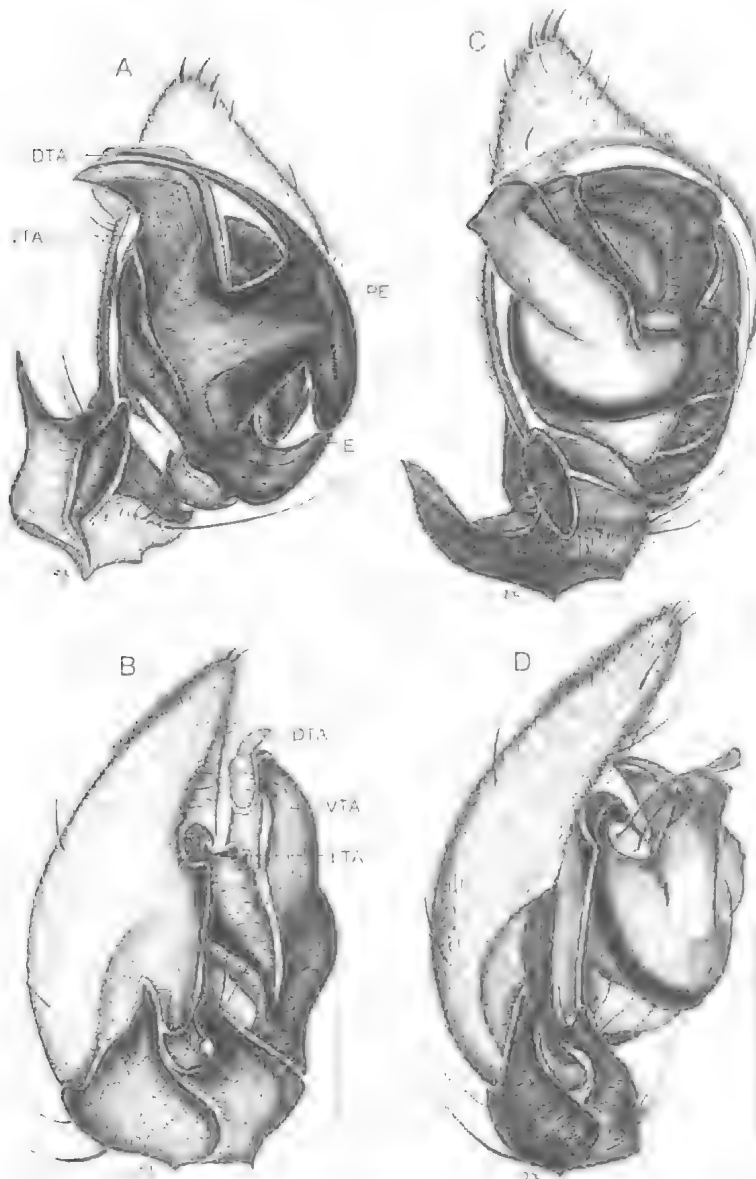


FIG. 5. *Pentasteron* spp. right male palps. A, B, *P. securifer*; A, ventral; B, retrolateral. C, D, *P. isobetae*; C, ventral; D, retrolateral. Scale 0.5mm. DTA = dorsal tegular apophysis, E = embolus, LTA = lateral tegular apophysis. VTA = ventral tegular apophysis.

***Pentasteron storosoides* sp. nov.**
(Figs 4D-F, 15)

ETYMOLOGY. Superficially like *Storos* Jocqué in its deep tibial concavity and strong ventral tibial knob.

MATERIAL. HOLOTYPE: ♂, 30km SW of Wilcannia, New South Wales, ca. 142°45'E, ca. 32°25'S, 22.xii.1998, black box fogging, U. & M. Baehr (QM S46948).

DIAGNOSIS. Males have a palp with a deep tibial concavity delimited by the large longitudinal ventrolateral swelling and a dorsolateral apophysis with recurved tip, in combination with the bifid embolar apophysis which gives the impression that the embolar complex is tritid.

DESCRIPTION. *Male* (holotype). Total length 4.88; carapace 2.46 long, 1.74 wide; tibia+patella 12.50.

Colour: Carapace chestnut brown; chelicerae and sternum medium brown; coxae white with dark brown rim; trochanters dark with yellow ventral patch; femora white with dark patches at base in proximal half, dark brown in distal half; remainder of legs yellowish brown, posterior tibiae with blackish lateral streaks. Abdomen shiny black; dorsum with two pairs of small white spots and 3 crescent-shaped spots in front of spinnerets; sides with one oblique white spot and pale mottling; venter sepia, with two yellow spots in front of epigastric fold. Carapace finely granulated; sternum smooth.

Eyes: a: 0.15; b: 0.12; c: 0.14; d: 0.14; e: 0.04; f: 0.02; g: 0.07; h: 0.14; AL-AL: 0.28. MOQ: AW = 1.00 PW; AW = 0.86 L. Clypeus 0.48 or 4 times AL. Chilum 0.10 high, 0.036 wide.

Spination:

	I	P	T	M
I	pl1d2	-	v2-2-2	v2-1-1
II	pl1d3	-	v1-2-2	v2-2dw3
III	pl2d2r1	pl1d1r1	pl2d2r1v2-2-2	10disp dw6
IV	pl2d5	pl1d1r1	pl3d3r1v2-2-2	10disp dw6

Hinged hairs: TI and TII: d1. Preening brush on Mt II and III.

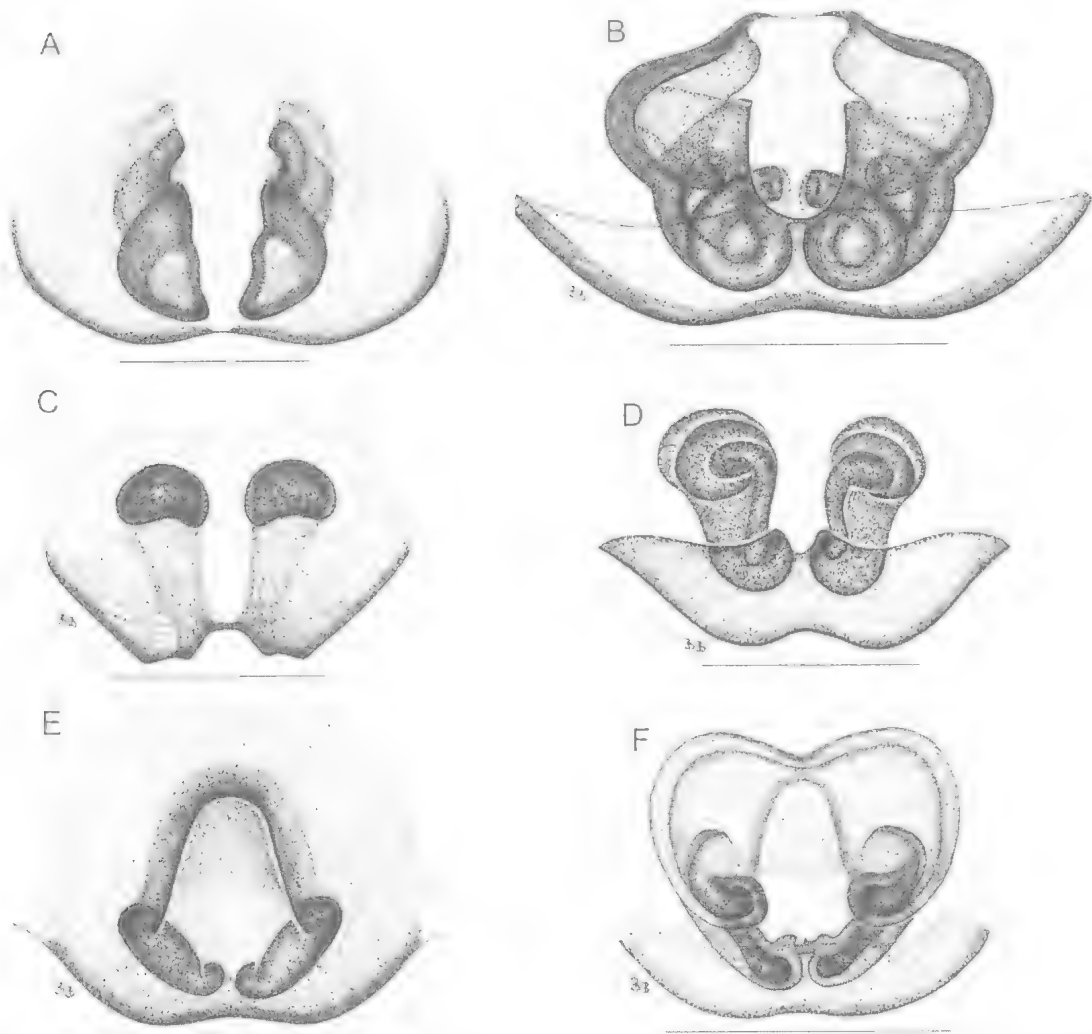


FIG. 6. *Pentasteron* spp. epigynes. A,B, *P. simplex*; A, ventral; B, dorsal (cleared). C,D, *P. oscitans*; C, ventral; D, dorsal. E,F, *P. intermedium* E, ventral; F, dorsal. Scale 0.5 mm.

Abdomen: anterior lip of tracheal spiracle not contrasting from rest of venter; posterior lip larger, sticking out, brownish yellow. Colulus a small swelling with 8 setae.

Male palp (Fig. 4D-F): tibia with large retrolateral concavity delimited by thick longitudinal ventrolateral swelling and large dorsolateral apophysis with strongly recurved tip; with short prolateral dorsal apophysis. Cymbium with shallow proximal fold and shallow basal concavity. Cymbial flange long, separated in front from cymbial rim by short bend. Tegulum broad at base, tapered toward fairly slender VTA; LTA short, thorn-shaped; DTA membranous, widened towards truncated,

serrated extremity. Embolus fairly short, fairly slender; EA with bifid tip, giving the embolar complex a trifid impression.

DISTRIBUTION. Known only from type locality.

***Pentasteron isobelae* sp. nov.**
(Figs 5C,D, 7C,D, 15)

ETYMOLOGY. In honour of Isobel Raven.

MATERIAL. HOLOTYPE: ♂, Ramornie SF, Track off Mt Tindal Rd. NSW, 29°42'S 152°38'E, 4.ii-9.iv.1993, 220m, M. Gray & G. Cassis (AM 039404). PARATYPES: New South Wales: 1 ♀, together with holotype; 1 ♀, NSW, 68AR, Maria River SF, NPWS survey, 1km along Northern Trail into rubbish dump, 31°08'S 152°28'E, 4.ii-9.iv.1993, 35m, M. Gray & G. Cassis (AM KS 039403);

1♂, Ramornie SF, Track off Mt Tindal Rd, 29°42'S 152°37'E, 4.ii-9.iv.1993, 220m, M. Gray & G. Cassis (NPWS survey) (AM KS039402); 1♂, Tindal Rd, 380m, further as previous (AM KS 039200); 1♂, 240 m east of junction of Kunderang East and Kunderang West Rds, 30°48'S 152°02'E, 4.ii-9.iv.1993, 900m, M. Gray & G. Cassis (NPWS survey) (AM KS039120); 1♂, Bundjalung National 20, near gravel quarry, 29°17'S 153°16'E, 4.ii-9.iv.1993, M. Gray & G. Cassis (AM KS 039198); 1♂, Chaelundi SF, 1.2km W along Stockyard Fire Trail from Chandlers Ck, 29°56'S 152°31'E, 450m, 4.ii-9.iv.1993, M. Gray & G. Cassis (AM KS 039199); SE Queensland: 2♂, Expedition Ra NP, Amphitheatre camp, 25°12'S 148°59'E, 14-19.xii.1998, 560m, open forest, G. Montheith, G. Cook & G. Thompson (QM S52611).

DIAGNOSIS. Male palp with a small cymbial concavity and ear-shaped embolar appendage; ♀♀ with large central depressions and an almost straight posterior margin of epigyne.

DESCRIPTION. *Male* (holotype; Pt in brackets). length 4.74 (4.46); carapace 2.30 (2.16) long, 1.62 (1.60) wide; tibia+patella I 2.22 (2.11).

Colour: Carapace chestnut brown; chelicerae medium brown; sternum medium brownish with darker lateral margins; coxae white; trochanters dark with yellow ventral spot; femora white in proximal half, dark brown in distal half; patellae yellow; tibiae yellow suffused with black on sides; metatarsi and tarsi yellow. Abdomen dark grey; dorsum with 2 pairs of small white spots followed by 2 white chevrons and spot with sinuous margins in front of spinnerets; sides with 1 white spot in front and 3 large oblique stripes; venter sepia with 2 small yellow spots in front of epigastric fold; lung covers yellow.

Carapace finely granulated; sternum smooth.

Eyes: a: 0.16; b: 0.12; c: 0.11; d: 0.12; e: 0.03; f: 0.03; g: 0.08; h: 0.10; AL-AL: 0.32. MOQ: AW = 1.06 PW; AW = 1.00 L. Clypeus 0.38 or 3.2 times ALE.

Chilum single 0.24 wide 0.08 high.

Spination:

	F	P	T	Mt
I	pl1d2	-	√2-2-2	2-2-2
II	d2	-	√2-2-2	√2-2 dw3
III	pl2d3rl1	pl1d1rl1	pl2d2rl3√2-2-2	10disp dw5
IV	pl1d4	pl1d1rl1	pl3d3rl3√2-2-2	10disp dw5

Hinged hairs: TII and TIII: d1. Preening brush on Mt II and III.

Male palp (Fig. 5C,D): femur and patella pale, contrasting with remainder of palp; tibia with large retrolateral concavity delimited along posterior end by solid, tapered and twisted, sharp-

tipped apophysis pointing forward and thin, truncated and slightly indented ventrolateral apophysis. Cymbium with shallow basal concavity according with tibial concavity; flange unmodified. Tegulum broad, with large, tongue-shaped terminal VTA. Embolus short, flat, rigid, slightly twisted, almost straight, accompanied by large, flat transparent ear-shaped apophysis, provided with 2 semicircular ridges; DTA membranous, narrow, straight.

Female (paratype). Total length 5.60; carapace 2.56 long, 1.70 wide; tibia+patella I: 2.53.

Colour: almost as in male but generally paler.

Eyes: a: 0.16; b: 0.15; c: 0.14; d: 0.15; e: 0.05; f: 0.03; g: 0.08; h: 0.15; AL-AL: 0.32. MOQ: AW = 1.00 PW; AW = 0.85 L.

Clypeus: 0.44 or 3.0 times ALE. Chilum single 0.23 wide, 0.11 high.

Legs: Spination:

	F	P	T	Mt
I	pl1d2	-	√2-2-2	√2-1-1-2
II	d2	-	pl2√2-2-2	√2-1-2 dw3
III	pl2d3rl1	pl1d1rl1	pl2d2rl2√2-2-2	10disp dw5
IV	pl1d3rl1	pl1d1rl1	pl3d3rl3√2-2-2	10disp dw5

Hinged hairs: TI d1, TII d1. Preening brush on Mt II and III.

Epigyne (Fig. 7C,D): simple: suboval sclerotised with almost straight posterior rim and 2 large central depressions. Copulatory ducts semicircular; spermathecae small, caudal, adjacent.

Variation: colour pattern and size very stable: ♂ carapace length 1.82-1.87, width 1.20-1.22; ♀ carapace 1.92-1.98 long, 1.33-1.40 wide.

DISTRIBUTION. SE Queensland and NSW.

Phenasteron gen. nov.

TYPE SPECIES. *Phenasteron longiconductor* sp. nov.

ETYMOLOGY. Greek *phenomenon* with *Asteron*; refers to 'phenomenal' male palps. Gender is neuter.

DIAGNOSIS. ♂♂ have an domed cephalothorax with highest point just in front of fovea (Fig. 9A), enormous T-shaped distal tegular apophysis (DTA) with refolded margin (Fig. 9B,D), course of the sperm-duct in the tegulum not transverse but oblique and the posterior sclerotised swelling of the subtegulum. ♀♀ unknown.

DESCRIPTION. Small spiders (2.90-3.5) with smooth or slightly granulate tegument. Carapace widest at level of coxae II (Fig. 8), narrowed to

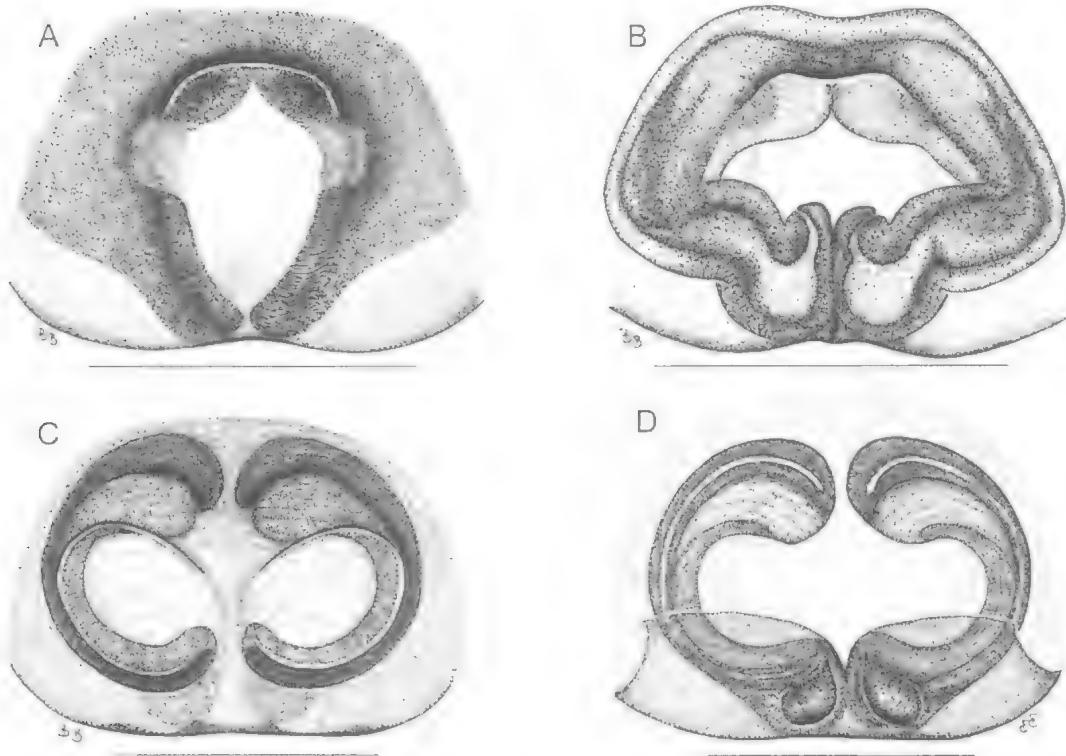


FIG. 7. *Pentasteron* spp. epigynes. A,B, *P. securifer*; A, ventral; B, dorsal (cleared). C,D, *P. isobelae*; C, ventral; D, dorsal. Scale 0.5mm.

0.60 maximum width in males. Profile domed with highest point just in front of fovea (Fig. 9A).

Colour: carapace orange to medium brown, chelicerae and sternum yellowish brown.

Eyes (Figs 8, 9A) in 3 rows (2-4-2). Only ALE in first row, second AME (in middle) and PLE, third only of PME. Eyes subequal or AME larger than remainder. MOQ slightly longer than wide. Clypeus slightly concave retreating, c. 5 times diameter of ALE; with few hairs. Chilum single, short and wide, without setae. Chelicerae as usual in the family with few hairs in front and dense row on distal promargin; no teeth. Labium narrowed at base; sparsely haired. Gnathocoxae rather elongate; sparsely haired; with anteromesal scopula. Sternum flat; triangular with slightly procurved anterior margin and slight triangular extensions between coxae. No inter- nor precoxal sclerites. Abdomen dark sepia with five pale spots.

Legs: formula 4123. Spination: few spines on pairs I, II, more numerous on III, IV. Paired tarsal claws with numerous (12-14) teeth. Unpaired claw on small onychium.

Trichobothria in 2 rows on T, single row on Mt and t. Hinged hairs few, restricted to dorsal side of T1 and II. Metatarsal preening brush on Mt II and III poorly developed.

Abdomen oval; with poorly developed translucent anterior scutum; with faint dorsal sigilla and small lateral frontal sigillum on sides. Spinnerets: AS, conical, with short distal segment; MS, PS small, in a row. Colulus represented only by some hairs. Tracheal spiracle ordinary, small.

Male palp (Fig. 9B-E): tibia with large retro-lateral concavity delimited by solid dorsolateral apophysis and ventrolateral apophysis, with swollen lateral margin provided with macrosetae or row of hairs. Cymbium unmodified, flange simple, area above it sclerotised and slightly concave. Subtegulum with backward extended swelling. Base of tegulum narrowed toward origin of embolus; course of seminal duct oblique, not transverse; VTA large; DTA very large, T-shaped, distal margin of transverse bar refolded. Embolus emerging on lateral part of tegulum, long and slender. LTA a small, short thorn, or reduced.

Females unknown.

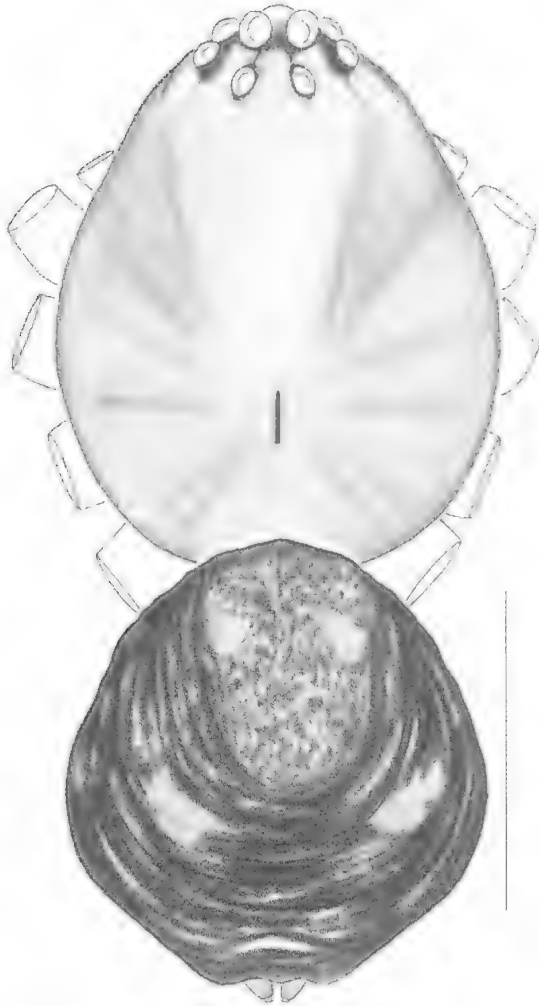


FIG. 8. *Phenasteron longiconductor* body dorsal. Scale 1mm.

KEY TO THE SPECIES OF *PHENASTERON*

1. DTA and embolus almost as long as bulbus; VTA with long slender distal prong, at right angle with body of this apophysis; course of sperm-duct longitudinal (Fig.9B,C) *P. longiconductor*
DTA and embolus much shorter than bulbus; VTA without slender distal part; course of sperm-duct oblique (Fig.9D,E) *P. machinosum*

Phenasteron longiconductor sp. nov. (Figs 8, 9A-C, 16)

ETYMOLOGY. Noun in apposition, refers to the very large DTA which appears to be the functional conductor.

MATERIAL. Holotype, ♂, 12.3km SSW of Murrayville P.O. Victoria 35°22'S 141°09'E; site 62, xi.1985, drift fence pitfall trap, A.L. Yen (VM). PARATYPES: Victoria:

1 ♂, 6.5 km SW of junction of MV highway and Annuello Rd., 34°50'S 142°34'E, site 11, x.1985, drift fence pitfall trap, A.L. Yen (VM); 1 ♂, 16 km SE of Murrayville, 35°22'S 141°19'E, site 71, xi.1985, drift fence pitfall trap, A.L. Yen (VM); 1 ♂, 15.5 km WSW of Hattah, 34°47'S 142°07'E, site 40, x.1985, drift fence pitfall trap, A.L. Yen (VM); WA: 1 ♂, Nanga station, 26°35'31"S 113°53'22"E 16.x.1994-19.i.1995 (WAM 99/2379), N. McKenzie & J. Rolfe, wet pits WAM/CALM Camarvon survey (NA5).

DIAGNOSIS. Males have an enormous pick-shaped tegular apophysis at embolus base.

DESCRIPTION. *Male* (holotype). Length 3.51; carapace 1.87 long, 1.31 wide; tibia+patella I 1.33 long.

Colour: Carapace medium brown with darker radiating striae and u-shaped darker pattern delimiting cephalic area; chelicerae and sternum medium reddish brown; coxae pale; trochanters pale with dark pro- and retrolateral spots; proximal half of femora white with dark proximal ring, distal half of femora II-IV medium brown suffused with black; femur I pale brown suffused with black; patellae uniform pale yellow; tibiae brownish yellow, darkened on ventral side. Abdomen dark sepia; dorsum with faint, narrow dark brown scutum in front and 5 white spots: 2 pairs in anterior half, and 1 spot in posterior half; 2 oblique white stripes on each side.

Carapace and sternum finely granulated. Highest point of profile halfway between fovea and PME.

Eyes: a: 0.12; b: 0.08; c: 0.08; d: 0.09; e: 0.03; f: 0.02; g: 0.10 h: 0.12; AL-AL: 0.28. MOQ: AW = 1.00 PW; AW = 0.87 L. Clypeus retreating, 0.34 or 4.2 times the diameter of an ALE.

Chilum single, 0.08 high, 0.18 wide.

Legs: Spination:

	F	P	T	Mt
I	d1	-	-	
II	d1	-	-	dw2
III	d2	pl1d1rl1	pl2d2rl2v2-2	4disp dw6

One hinged hair on tibiae I and II.

Male palp (Fig. 9B,C): tibia with large retrolateral concavity delimited by 2 apophyses: ventrolateral one, lamellate with sharply bent distal tip and ventrolateral haired ridge, dorso-lateral one long, gradually tapered, sharp. Cymbium dorsoventrally flattened, ventrally glabrous; basally shallowly concave; with retrolateral haired ridge and long flange distally curved and swollen. Subtegulum extended backwards, swelling strongly sclerotised, reaching special

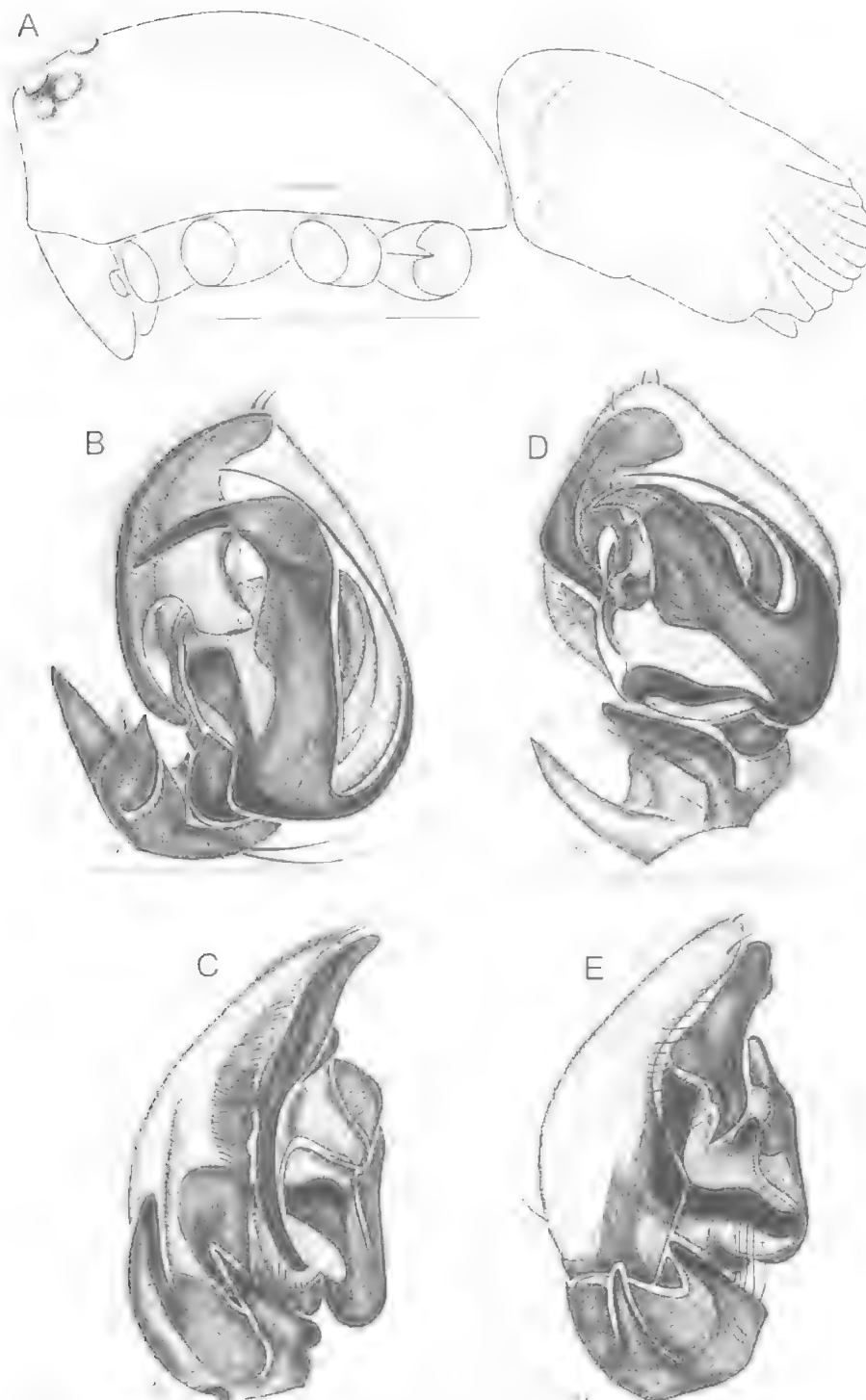


FIG. 9. *Phenasteron* spp. A-C, *P. longiconductor*; A, body lateral; B, C, right ♂ palp; B, ventral; C, retrolateral. D, E, *P. machinosum*, right ♂ palp; D, ventral; E, retrolateral. Scales, B, 1mm; D, 0.5mm.

concavity of tibia; tegulum broad at base, spermi-duct slightly bent backward. Embolus about as long as cymbium, fairly slender, curved outward. VTA very large, pick-shaped; base long, broad distal part turned outwards over more than 90°, short, sturdy; DTA very large; retrolateral margin rebordered, anterior prong broad and rounded, posterior prong long, tapered toward blunt apex.

Female unknown.

Size, colour pattern and spination very stable.

DISTRIBUTION. Victoria and WA.

***Phenasteron machinosum* sp. nov.**
(Figs 9D,E, 16)

ETYMOLOGY. Latin: *machinosus*, provided with tools; refers to the tool-shaped palpal sclerites.

MATERIAL. HOLOTYPE: ♂, South Gap Station, Beda Hill, Sth Aust, 31°51'S 137°37'E; 4-6.xii.1989, pitfall trap, D. Hirst (SAMA N199296).

DIAGNOSIS. Males with large shovel-shaped tegular apophysis (VTA) at embolus base; subtegulum with backwardly extended posterior swelling.

DESCRIPTION. *Male* (holotype). Total length 2.90; carapace 1.42 long, 1.12 wide; tibia+patella 1.06 long.

Colour: Carapace orange brown with faint darker radiating striae and u-shaped darker pattern delimiting slightly paler cephalic area; chelicerae and sternum pale yellowish brown, sternum darkened along margin; coxae pale; trochanters pale with dark pro- and retrolateral spots; proximal half of femora white with dark proximal ring, distal half of femora pale yellow suffused with black on sides; tibiae I and II pale yellow and suffused with black on venter and sides in proximal half, pale in distal half; tibiae III and IV pale yellow, suffused with black on venter and sides; metatarsi yellow; tarsi orange yellow, darkened towards tip. Abdomen dark sepia; dorsum with faint, narrow dark brown scutum in front and 5 white spots: 2 pairs in anterior half, and 1 spot in posterior half; 2 oblique white stripes on each side.

Carapace and sternum finely granulated. Carapace fairly high, highest point of profile just in front of fovea.

Eyes: a: 0.09; b: 0.08; c: 0.07; d: 0.06; e: 0.02; f: 0.01; g: 0.08 h: 0.10; AL-AL: 0.18, MOQ: AW = 0.18 PW; AW = 0.75 L.

Clypeus slightly retreating, 0.28 or 3.5 times ALE, Chilum single: 0.10 high, 0.28 wide.

Spination:

	I	II	III	IV
I	d1	-	s2-1	s2
II	d2	-	s1	s2
III	d2	pl1d1r1	pl2d2l2: 1-2	5disp dws
IV	d2	pl1r1r1	pl2d2r2s 1-12 2	7disp dws

One dorsal hinged hair on tibiae I, II.

Male palp (Fig. 9D,E): femur pale with dark retrolateral patch, patella pale, contrasting with rest of palp; tibia with large retrolateral concavity delimited by two apophyses; ventrolateral one fairly flat with group of strong setae; dorsolateral one ridge-shaped with sharp, proximal prong, slightly curved forward. Cymbium with thin but well developed retrolateral flange in proximal half. Embolus about half as long as cymbium, fairly slender, curved outward. VTA large, in shape of curved shovel, base fairly broad but narrower than distal part ending in slightly curved, distally rebordered flat part. DTA large; retrolateral margin strongly rebordered, anterior prong broad, rounded, posterior prong fairly short, sharp, curved inward.

Female unknown.

Colour pattern and spination very stable.

DISTRIBUTION. Known only from type locality.

***Leptasteron* gen. nov.**

TYPE SPECIES. *Leptasteron platyconductor* sp. nov.

ETYMOLOGY. Greek leptos, hidden with *Asteron* refers to this genus remaining hidden in the *Asteron*-complex. Gender is neuter.

Baehr & Jocqué (1996) mentioned these taxa as the *brachyconductor*-group.

DIAGNOSIS. Males have flat cephalothorax, elongate flat cymbium, large distal tegular apophysis (DTA) with refolded margin, spermi-duct in the tegulum not transverse but longitudinal and posterior sclerotised swelling of the subtegulum. Females unknown.

DESCRIPTION. Small to medium-sized (4.80-6.60) with smooth or slightly granulate tegument. Carapace widest at level of coxae II, narrowed to 0.65 max. width in ♂♂. Profile flat with highest point just behind PME (Fig. 11A).

Colour: variable; carapace colour varies from dark brown (*L. platyconductor*) to bright yellow (*L. vexillum*), chelicerae and sternum and legs uniform legs (*L. vexillum*) or with contrasting leg segments (*L. platyconductor*). Abdomen dark sepia with five pale spots. Sclerotised in front of

epigastric fold (*L. platyconductor*) or with pale booklung opercula (*L. vexillum*).

Eyes (Figs 10A,B,11A) in 3 rows (2-4-2). ALE only in first row, second with AME (in middle) and PLE, the third of PME. Eyes subequal or AME larger than remainder. MOQ slightly longer than wide. Clypeus straight or slightly retreating, 2.5 to 4 times diameter of ALE; with few hairs. Chilum single (*L. vexillum*) or double (*L. platyconductor*). Chelicerae as for family with a few hairs in front and a dense row on distal promargin; no teeth. Labium narrowed at base; sparsely haired. Gnathocoxae rather elongate; sparsely haired; with anteromesal scopula. Sternum flat; triangular with straight anterior margin and slight triangular extensions between coxae. No inter- nor precoxal sclerites.

Legs: formula 4123. Spination: few spines on pairs I, II, more numerous on III, IV. Paired tarsal claws with numerous (12-14) teeth. Unpaired claw on small onychium.

Trichobothria in two rows on T, single row on Mt and T. Hinged hairs present but few, restricted to dorsal side of T1 and II. Metatarsal preening brush on Mt II and III poorly developed.

Abdomen oval; with poorly developed translucent anterior scutum; with (*L. platyconductor*) or without (*P. vexillum*) dorsal and lateral sigilla. Spinnerets: AS, conical, with very short distal segment; MS and PS small, in a row. Colulus represented only by some hairs. Tracheal spiracle hidden by well developed anterior lip.

Male palp (Fig. 11B-E): tibia with a large retro-lateral concavity delimited by a solid dorsolateral apophysis and ventrolateral apophysis, with swollen lateral margin provided with macrosetae or row of hairs. Cymbium elongate, flat, flange simple, area above it sclerotised and slightly concave. Subtegulum with backward-extended swelling. Base of narrowed tegulum toward origin of embolus; course of seminal duct longitudinal, not transverse; VTA large, either wide and with large recurved extremity or long and slender. Embolus emerging on posterior part of tegulum, very long and slender. LTA small: knob-shaped; DTA very large, membranous or sclerotised; distal margin refolded.

Females unknown.

KEY TO THE SPECIES OF *LEPTASTERON*

1. Carapace uniform yellow; DTA membranous, T-shaped; VTA long and slender (Fig. 11D-E) *L. vexillum*
Carapace uniform dark brown; DTA sclerotised, sickle-shaped, VTA not long and slender but sharply bent (Fig. 11B,C) *L. platyconductor*

Leptasteron platyconductor sp. nov. (Figs 10A,11A-C,16)

ETYMOLOGY. Noun in apposition; refers to wide flat DTA which appears to be the functional conductor.

MATERIAL. HOLOTYPE: ♂, Cape Range, WA, 22°05'S 114°00'E; 14.iii-6.v.1992, pitfall trap outside cave C56, R.D. Brooks (WAM BES:1103). PARATYPE: 1♂, Station Creek, 127 km SSE Leinster, Western Australia, 28°45'S, 121°00'E, 8-9.xi.1987, M. Baehr (QM S45244).

DIAGNOSIS. Males with elongate palpal cymbium and very broad, large DTA (Fig. 11B); uniform dark colour.

DESCRIPTION. *Male* (holotype, paratype in brackets). Total length: abdomen missing in holotype (6.60); carapace 3.11 (3.10) long, 2.04 (2.02) wide; tibia+patella I 2.85 (2.80) long.

Colour: Carapace dark brown with darker radiating striae and v-shaped darker pattern in front of fovea; chelicerae and sternum dark brown; coxae, trochanters and femora dark brown with some darker stripes; tibiae medium brown with darker ventral side; metatarsi and tarsi brownish yellow. Abdomen dark sepia with five small white spots two in front, two in middle, one in front of spinnerets. Sides sepia, mottled with pale; venter pale sepia; two pale spots in front of epigastric fold; lung covers yellow.

Carapace and sternum smooth. Carapace fairly flat, highest point of profile just behind PME, provided with sparse but evenly dispersed cover of tiny setae.

Eyes: a: 0.16; b: 0.14; c: 0.17; d: 0.14; e: 0.04; f: 0.02; g: 0.08 h: 0.12; AL-AL: 0.30. MOQ: AW = 0.86 PW; $\Delta W = 0.82$ L. Clypeus slightly retreating, 0.70 or 5.0 times diameter of ALE.

Chilum double: each part 0.12 high and 0.28 wide.

Legs: Spination:

	I	P	T	Mt
I	pl1d2	-	v2-1-2	v2-1-1-2
II	d2	-	pl1v1-1-2	v2-1-1dw2
III	pl3d2rl2	pl1d1rl1	pl2d2rl2v2-2-2	8disp dw6
IV	pl2d3rl2	pl1d1rl1	pl3d2rl3v2-2-2	8disp dw6

One hinged hair on tibiae I and II. Preening brush on Mt II and III.

Abdomen with 2 round dorsal sigilla and an elongate lateral one in front on either side. Tracheal spiracle with swollen anterior lip and sclerotised protruding posterior lip. Colulus a group of about 8 short setae.

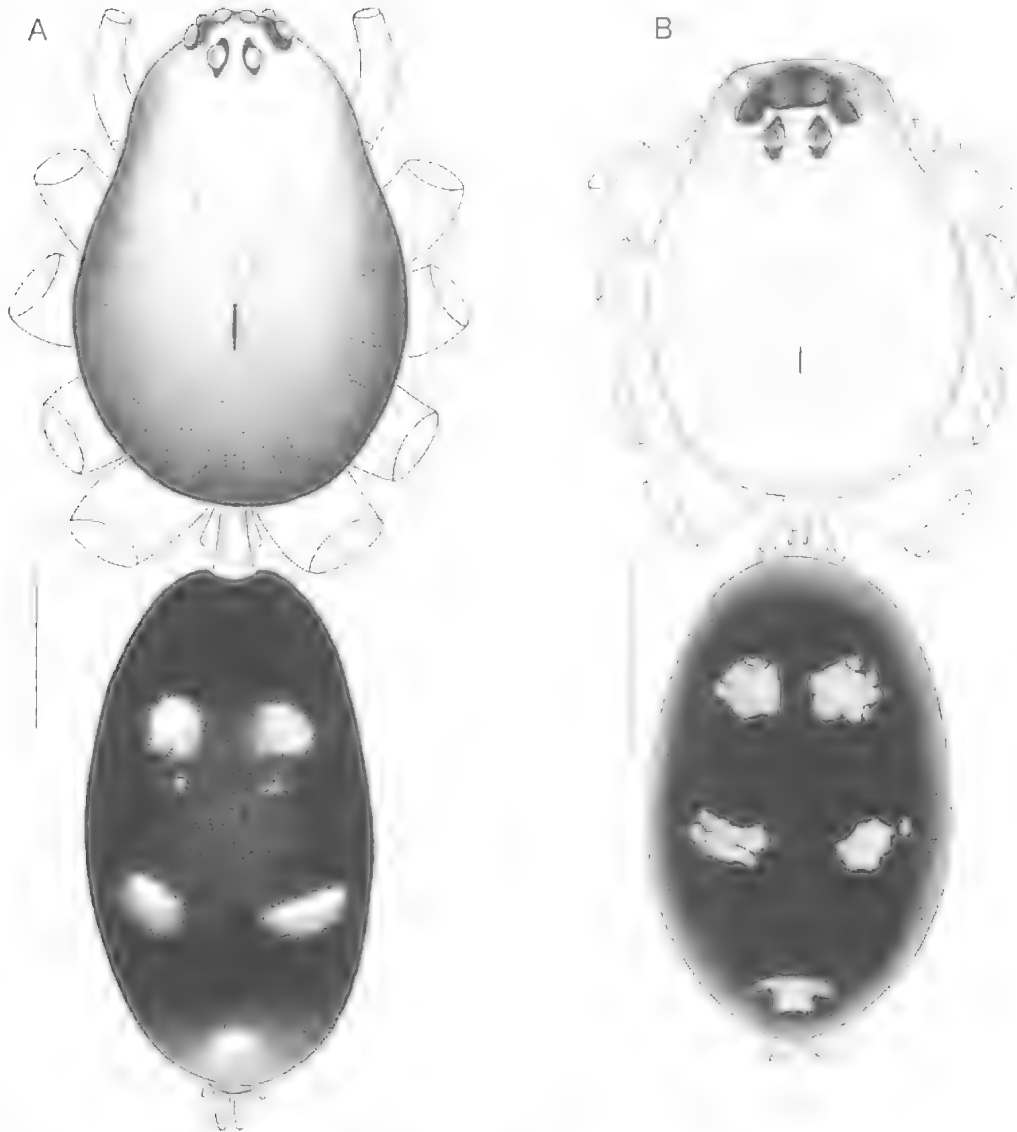


FIG. 10. *Leptasteron*. body dorsal. A, *L. platyconductor*. B, *L. vexillum*. Scale 1mm

Male palp (Fig. 11B,C): tibia with large retrolateral concavity delimited by two apophyses: ventrolateral one, lamellate with blunt, rebordered, frontal extension provided with some large setae; dorsolateral one with proximal, tapered, sharply pointed prong, with triangular tooth at frontal base. Cymbium elongate, dorsoventrally flattened, long, flange fairly long, slightly concave at base; retrolateral ridge provided with hairs standing out. Embolus very long, whip-like, originating on posterior part of tegulum with base pointing backward;

tegulum with long retrolateral ridge, ending in slender proximal knob; VTA large, basal part broad and concave, sharply curved outward at about half its length, ending in long, tapered prong; DTA large, very wide, broadly curved, rebordered along retrolateral edge.

Female unknown.

Variation: the two known males are very similar.

DISTRIBUTION. Known only from type locality.

Leptasteron vexillum sp. nov.
(Figs 10B, 11D,E, 16)

ETYMOLOGY. Noun in apposition; Latin; *vexillum*, flag; referring to the large DTA.

MATERIAL. HOLOTYPE: ♂, Tindery Nature Res., southern entrance, NSW, 35°39'39"S 149°12'43"E, 14.iii.1999, J. Tarnawski & S. Lassau, CBCR003-032 (AM KS 55882).

DIAGNOSIS. Males are unique in palp with enormous, terminal folded DTA, very long VTA and long whip-like embolus.

DESCRIPTION. *Male* (holotype). Total length 4.86; carapace 2.24 long, 1.64 wide, tibia+patella 1.232.

Colour: Carapace uniform yellow with small dark area on either side above condyle of yellow chelicerae; sternum pale yellow; femora yellow turning to orange distad; rest of legs orange. Abdomen dark grey, with orange tinge above pedicel; with two pairs of white spots and smaller triangular spot in front of spinnerets; sides and venter pale; area in front of epigastric area yellow.

Teguments smooth. Highest point of carapace just behind PME. Carapace and legs provided with sparse but evenly dispersed cover of tiny setae.

Eyes: a: 0.16; b: 0.14; c: 0.14; d: 0.14; e: 0.04; f: 0.04; g: 0.08; h: 0.08; AL-AL: 0.20 MOQ: AW = 1.00 PW; AW = 0.90 L. Clypeus slightly retreating, 0.34 high or 2.5 times diameter ALE.

Chilum single: 0.14 high, 0.18 wide.

Legs: Spination:

	F	P	T	Mt
I	d1	-	v2-2-2	v2-2 dw3
II	d	-	v1-2-2	v2-2 dw3
III	pl2d3rl2	pl1d1rl1	pl2d2rl1 v2-2-2	8disp dw5
IV	pl1d3rl1	pl1d1rl1	pl2d2rl2 v2-2-2	8disp dw5

Hinged hairs: one dorsal on TI and II.

Epigastric area with triangular indentation. Large sclerotised area in front of tracheal spiracle with pronounced frontal lip. Colulus a row of setae.

Male palp (Fig. 11D,E): tibia with large retrolateral concavity delimited dorsally by long, forward -directed slightly downcurved pointed apophysis, ventrally by slightly shorter, straight, pointed apophysis; prolaterally swollen with 2 macrosetae. Cymbium crescent-shaped, strongly tapered; tegulum with caudal, flattened extension bearing long, whip-shaped embolus which

originates on posterior part of tegulum. Long, slender, outward curved VTA originates on prolateral tegular ridge. DTA large, membranous, broad extremity with large fold accommodating extremities of both VTA and embolus.

Female unknown.

DISTRIBUTION. Known only from type locality.

Subasteron gen. nov.

TYPE SPECIES. *Subasteron daviesae* sp. nov. (Fig. 14) Image from D. Knowles, mentioned in Lindsey (1998) as knobble spider.

ETYMOLOGY. *Subasteron*, is referring to the slightly aberrant somatic morphology of the single species in this genus as compared to other members of the *Asteron*-complex.

DIAGNOSIS. Recognised by the peculiar shape of the cephalothorax which reaches its highest point at the level of the PME and the accordingly high clypeus, up to ten times the diameter of the ALE. Further diagnostic characters are from male palp, first the presence of a prolateral tegular apophysis (PTA) which is unique in the *Asteron*-complex: tibia has a deep retrolateral concavity combined with more or less pronounced concavity on base of cymbium; cymbium has a prolateral basal extension fitting in a concavity with membranous bottom of tibia.

DESCRIPTION. Medium-sized spiders (7.00-9.00) with very finely granulate tegument. Carapace widest at coxae II (Fig. 12A), slightly narrowed to 0.8 maximum width in females, to ca. 0.68 maximum width in males. Profile raised toward front with highest point near PME (Fig. 12C); fovea deeper in males than females.

Colour: carapace and sternum dark brown, chelicerae medium brown; legs with strongly contrasting, white to dark brown segments: coxae pale, trochanters dark, femora dark brown and white, tibiae brown with darker stripes; metatarsi pale, medium brown in distal part in females, uniform dark brown in males; tarsi brownish orange. Abdomen dark with contrasting pattern of white spots and patches. Males darker and with more contrasting pattern.

Eyes (Fig. 12C,D) in 3 rows (2-4-2). ALE only in first row, second with AME (in the middle) and PLE, third with PME. Eyes subequal but ALE smaller than others. MOQ longer than wide. Clypeus slightly concave, high, 6 times ALE in females, 10 times ALE in males; with some setae. Chilum double; separation not complete in

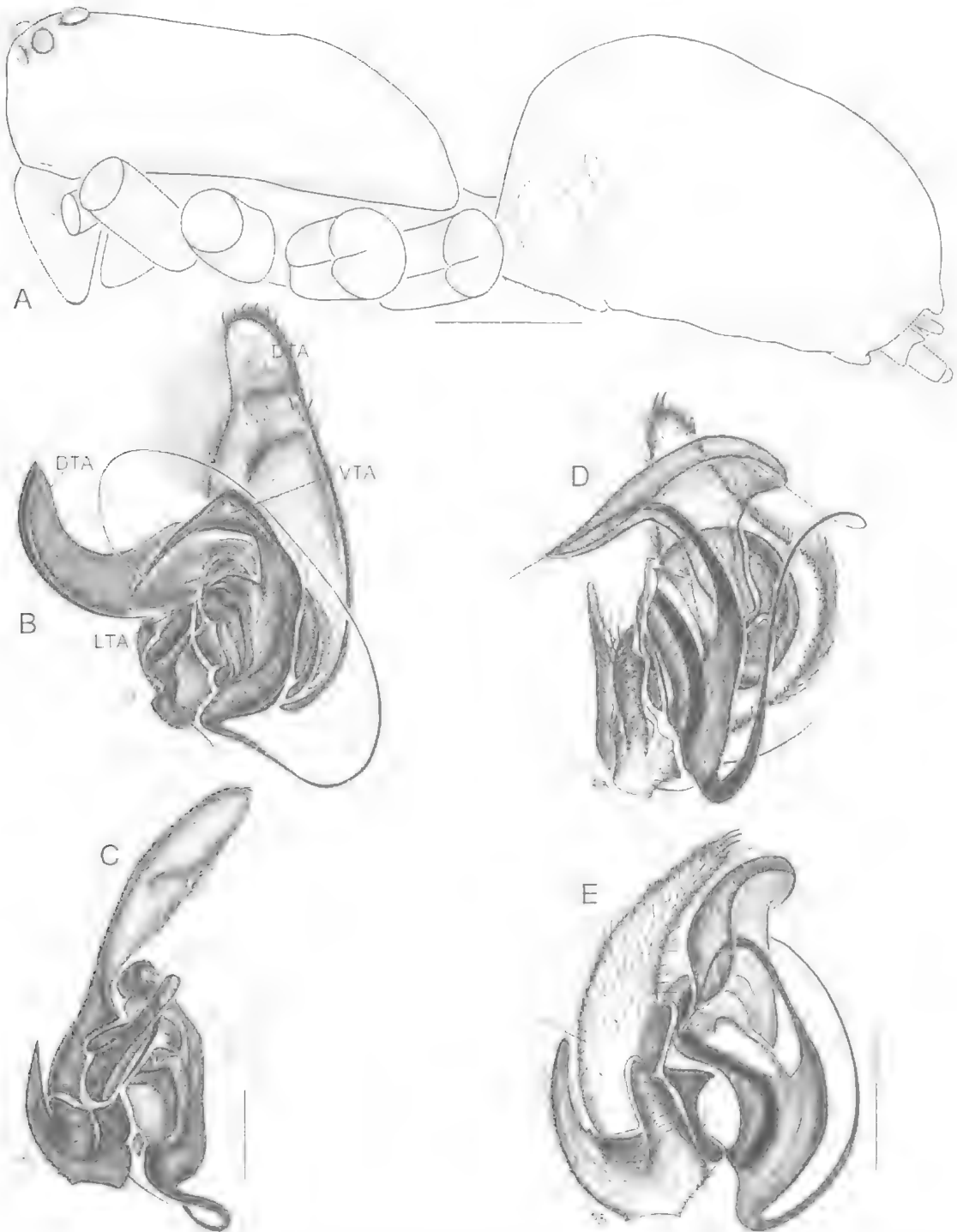


FIG. 11. *Leptasteron* spp. A-C, *L. platyconductor*; A, body lateral; B,C, right male palp; B, ventral; C, retrolateral. *L. vexillum*; D,E, right male palp; D, ventral; E, retrolateral. Scales, C, 1mm; E, 0.5mm. DTA = dorsal tegular apophysis, LTA = lateral tegular apophysis, VTA = ventral tegular apophysis.

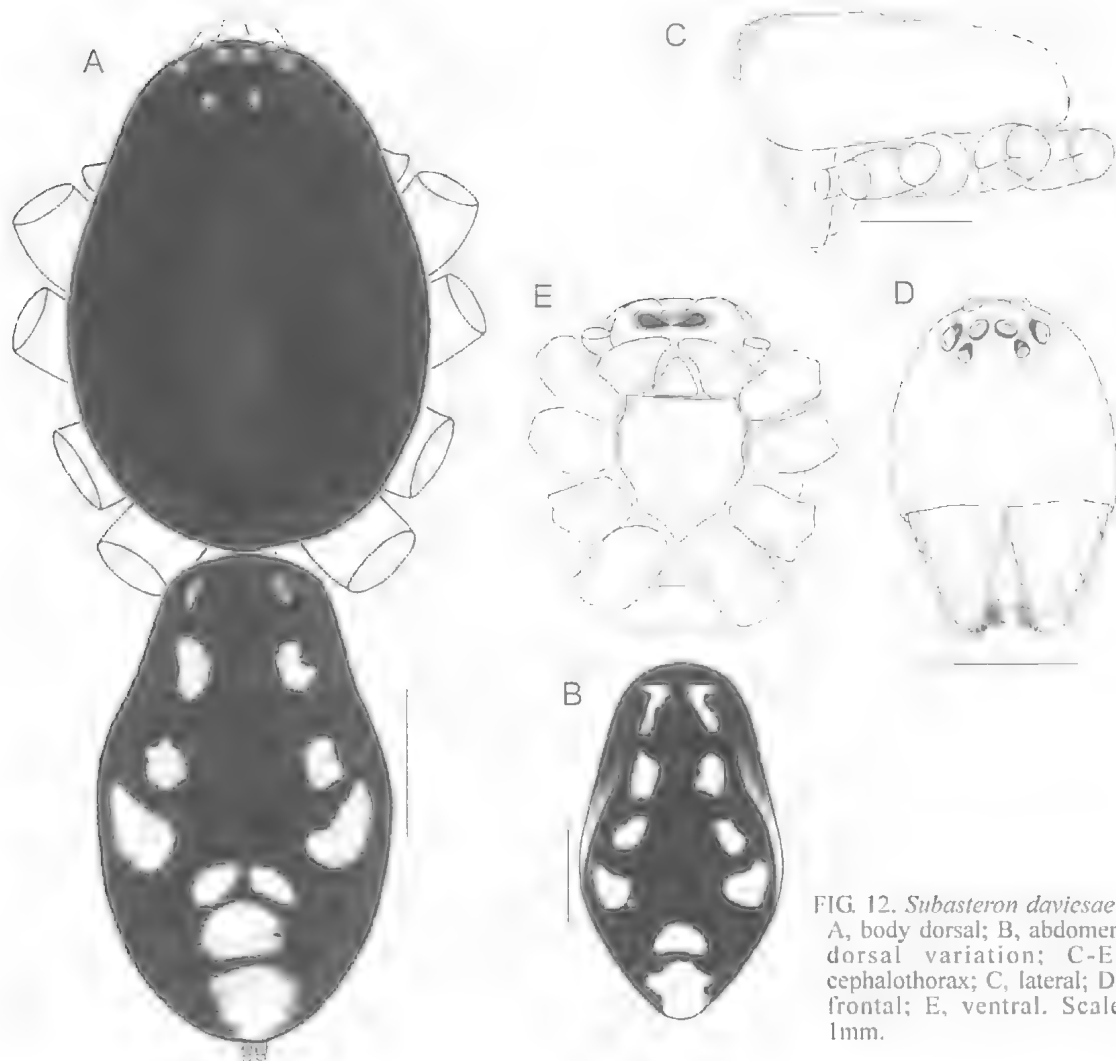


FIG. 12. *Subasteron daviesae*: A, body dorsal; B, abdomen dorsal variation; C-E, cephalothorax; C, lateral; D, frontal; E, ventral. Scale 1mm.

superior half; without setae. Chelicerae as usual in the family with few hairs in front and dense row on distal promargin; no teeth. Labium narrowed at base; sparsely haired. Gnathocoxae rather elongate; sparsely haired; with anteromesal scopula. Sternum flat; triangular with anterior margin slightly concave; with very small triangular extensions between coxae. No inter- nor precoxal sclerites.

Legs: formula 4123. Spination: spines fairly long; up to 4 times of diameter Mt IV in ♂♂, 2.5 times diameter of Mt IV in females; few spines on pairs I and II, more numerous on III and IV. Paired tarsal claws with numerous (12-14) teeth on anterior leg pairs, with slightly fewer on those

of legs III and IV. Unpaired claw toothless, on small onychium.

Trichobothria in 2 rows on T, single row on Mt and t. Hinged hairs few, restricted to dorsal side of T1 and II. Metatarsal preening brush on Mt II, III and IV, poorly developed.

Abdomen oval, fairly elongate; in males with marked central dip; with 2 dorsal sigilla, poorly developed elongate frontal sigillum on either side and pair just behind epigastric gold, more strongly developed in ♂♂. Spinnerets: AS, fairly long, slightly conical, with very short distal segment; MS and PS very short, absent in ♂♂. Colulus represented by group of setae. Tracheal spiracle hidden by well developed anterior lip.

Male palp (Fig. 13A-C): tibia with large retrolateral concavity delimited by solid dorsolateral apophysis and ventrolateral apophysis, with swollen lateral margin and frontal tooth. Cymbium with well developed flange and shallow concavity, several spines near distal tip. On prolateral side with basal extension fitting in concavity with membranous bottom of the tibia. Subtegulum strongly developed; partly membranous. Tegulum with broad base carrying transverse section of seminal duct; behind it partly membranous, partly strongly sclerotised; VTA small but strongly sclerotised; with strong prolateral apophysis more or less parallel with embolus. Embolus emerging on prolateral part of tegulum, short, rigid, curved outward. DTA strongly developed, sclerotised. LTA, flat, thorn-shaped.

Epigyne (Fig. 13D,E): strongly sclerotised plate with central depression and roughly rectangular plate with rounded anterior margin. Internal structure obscure due to strong sclerotisation: entrance ducts starting near centre running toward the front then along sides backward enter simple, thick-walled spermathecae near centre. Female palp with finely toothed claw.

Subasteron daviesae sp. nov.
(Figs 12A-E, 13A-E, 14, 16)

ETYMOLOGY. In honour of Val Davies, one of the collectors and in recognition of her important work on Australian spiders.

MATERIAL. HOLOTYPE. ♀, SEQ, 3669, Kroombit Tops, Lower Dry Creek, 45km SSW Calliope, Queensland, 9.19.xii.1983 1000m, open forest, V. Davies & J. Gallon (QM S3669). PARATYPES: Queensland: 4 ♂, 1 ♀, together with holotype. 1 ♂, SEQ, Braemar SE, 27°13'S 150°50'E, 4-8.ii.1980 R. Raven & QM (QM S3668); 1 ♂ 1 ♀, SEQ, Kroombit Tops, northern escarpment, 45 km SSW Calliope, 9-19.xii.1983, open forest, v. Davies & J. Gallon (QM S4429); 1 ♂, xii.1983, B. Jahnke, further as previous (QM S4415); 1 ♂, SEQ, Clear Mt., Samsonvale Lake, 27.xii.1984, G. Anderson (QM S4275); 2 ♂, NQ, Cairns, 1968, C. Coleman (AM KS15719); 1 ♂, SEQ, Numinbah ST, 28°12'S 153°13'E, xi.1979, under bark, T. Robinson (QM S3822); 1 ♂, SEQ, Fraser Island National Park HQ, 14.x.1978 (QM S3767); 1 ♂, Stony Ck. via Samford, 27°20'S 152°48'E, 2.II-6.IV.1996, H. Janetzki & G. Monteith (QM S37773); 1 ♂, SEQ, Clear Mt., Samsonvale, 27.xii.1984, G. Anderson (QMS 4275); 1 ♂ 1 ♀, SEQ, Gurgeena Plateau, open forest, 25°27'S 151°22'E, 10.x.-19.xii.1998, intercept trap 360m, 7511, G. Monteith & G. Cough (QM S47507); 1 ♂, SEQ, Gurgeena Plateau, evergreen forest, 25°27'S 151°23'E, 10.x.-19.xii.1998, intercept trap, 360m 7513, G. Monteith & G. Cough (QM S47508).

DIAGNOSIS. Males have a unique combination of sclerites in palp: particularities of cymbium with a prolateral basal extension and of bulbus with poorly developed VTA, large DTA and mostly very well developed prolateral tegular apophysis (PTA).

DESCRIPTION. *Male* (holotype). Length 7.96; carapace 3.82 long, 2.60 wide; tibia+patella 14.38.

Colour: carapace dark brown with very faint dark radiating striae and V-shaped dark mark in front of fovea. Chelicerae and sternum medium brown, slightly suffused with black. Coxae pale with dark, distal, prolateral triangles; trochanters medium brown with darker lateral spots; femora each with different contrasting black and white pattern, obliquely divided between upper and lower parts; patellae medium brown, anterior one dorsally pale, second one with pale dorsal spot; tibiae medium brown, first one with pale dorsal side, second and fourth with pale proximal, dorsal spot; metatarsi medium brown, paler towards proximal end; tarsi yellowish orange. Abdomen dark sepia to black; dorsum with 10 pale spots; 8 in 4 pairs, 2 in front of spinnerets; frontal pair reniform, second and third pair small and oval, fourth pair large, rounded; central spots in front of spinnerets elongate; sides with large, oblique, drop-shaped white patch; venter with a pair of rounded white spots on pale sepia background.

Carapace and sternum smooth.

Eyes: a: 0.10; b: 0.14; c: 0.18; d: 0.18; e: 0.04; f: 0.16; g: 0.20; h: 0.24; AL-AL: 0.26. MOQ: AW = 0.71 PW; AW = 0.63L

Clypeus: 1.0 or 7.1 times diameter of ALI. Chilum double each part 0.32 large, 0.14 high.

Legs: Spination:

	F	P	I	Ab
I	pl1a3rl1	pl1	pl2x2-2-2	dw3
II	pl3d4rl3	pl1	pl1x2-1-2	dw3
III	pl1a1-1	pl2-1	pl2x2-2-2	dw3
IV	pl1a1-1	pl1-1	pl2x2-2-2-2	10dispdw5

One dorsal hinged hair on tibiae I and II, several macrosetae on ventral femora.

Male palp (Fig. 13A-C): tibia with large retrolateral concavity delimited by swollen ventrolateral apophysis provided with pointed anterior part; dorsolateral apophysis with slightly ridged prong directed forward. Cymbium with well developed rebordered flange. Embolus fairly short and rigid, well delimited from

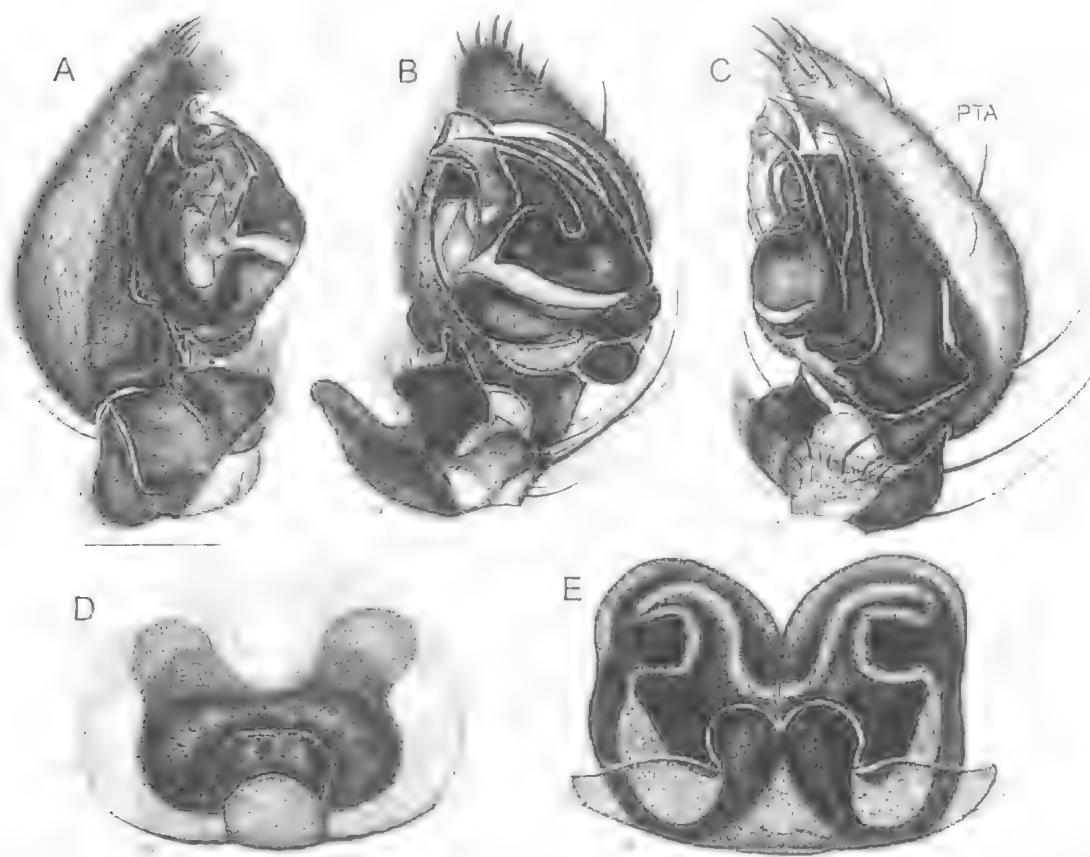


FIG. 13. *Subasteron daviesae*. A-C, right male palp; A, ventral; B, retrolateral; C, prolateral; D, E, epigyne; D, ventral; E, dorsal. Scales 0.5mm. PTA = prolateral tegular apophysis.

tegulum; VTA hardly developed, nothing more than a shallow prominence near base of embolus; LTA a membranous thorn-like appendage; DTA broad, curved, broadened towards extremity, concave in ventral view; PTA well developed, originating on dorsal part of tegulum separated from ventral part by shallow cleft; shape similar to that of embolus, but no embolar apophysis, like in *Pentasteron* ssp.

Female (Fig. 13D,E). Total length 9.00; carapace 3.60 long, 2.40 wide; tibia+patella I 3.30.

Colour: very much as in male but less dark and contrast less strong. Palp pale yellow with distal part of femur and tarsus medium brown.

Carapace and sternum smooth.

Eyes: a: 0.14; b: 0.12; c: 0.14; d: 0.16; e: 0.06; f: 0.12; g: 0.22; h: 0.22; AL-AL: 0.30. MOQ: AW = 0.64 PW: AW = 0.64.

Clypeus: 1.11 or 9.2 times diameter of ALE. Chilum double each part 0.42 large, 0.16 high.

Legs: Spination:

	F	P	T	Mt
I	pl1d3r1	-	pl1v2-2-2	v2-2-2dw3
II	pl3d3r12	pl1	pl1v1-2-2	v2-1-1-1dw3
III	pl4d4r13	pl2r1	pl2d2r12v2-2-2	8disp dw6
IV	pl2d4r11	pl2r1	pl2d2r13v2-2-2	10disp dw5

One dorsal hinged hair on tibiae I and II, several macrosetae on ventral side of femora.

Epigyne (Fig. 13D,E): central part strongly sclerotised and almost black, provided with two narrow copulatory openings; posteriorly with paler part. Copulatory ducts run around epigyne margin, ending in small touching spermathecae.

Variation: male size stable TL: 6.9-8.0; carapace length: 3.2-3.9, carapace width: 2.4-2.7. Colour pattern with slight variations: dorsal spots in front of spinnerets sometimes with transverse or longitudinal divisions or sometimes completely fused and forming one large white patch. Clypeus in male up to 10 times diameter of



FIG. 14. *Subasteron daviesae*, body dorsal, slide from Knowles.

ALE; discrepancy is mainly due to delimitation of ALE since height of clypeus appears stable.

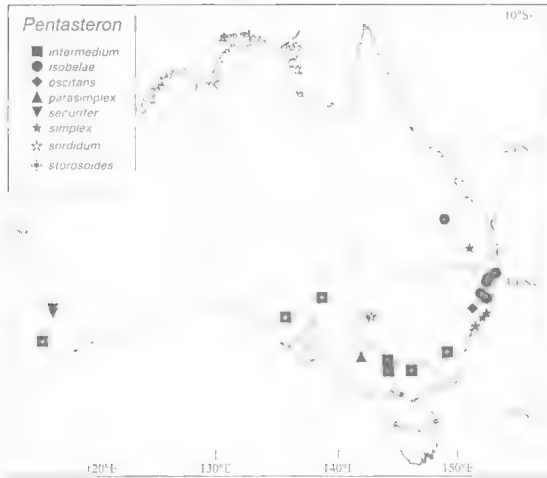
DISTRIBUTION. Queensland.

DISCUSSION

Including species described herein, the *Asteron*-complex now contains 37 species in 7 genera. *Asteron mas* Jocqué, 1991 was not included in the revision of *Asteron* ss. as it belongs in another genus of the complex but keeps its binomen until the new speciose genus where it belongs is described.

As stated in the introduction separation of the genera erected herein was problematic. Phylogenetically basal taxa are often difficult to define due to the lack of synapomorphies. Jocqué (1991) described a number of Australian zodariid genera almost exclusively based on palpal morphology. Jocqué (1995a,b) erected a few more genera and

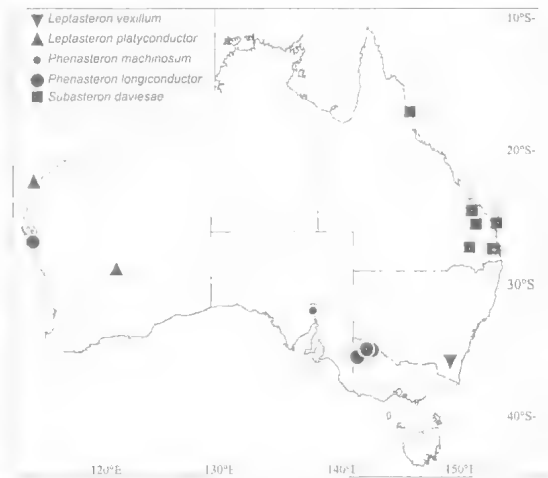
foreshadowed more supraspecific taxa for the wealth of Australian zodariids. Definition of the genera will continue to be almost exclusively based on genitalia. Somatic characters are often stable within these taxa but they do not offer a reliable base, as they appear to be plesiomorphic or extremely homoplastic characters. Examples in the present paper are the shape of the carapace (clypeus height), and of the chilum (single, double), eye arrangement (proportions of MOQ), colour pattern, shape of tracheal spiracle. Definition of genera in the Australian zodariids and in that family in general, has therefore mainly been based on genitalia. Yet, the epigyne of these species is especially hard to study, mainly because of the thickness and strong sclerotisation of its internal structure. Also the epigyne is usually structurally simple offering few characters. In this group, ♂ palps therefore

FIG. 15. Records of *Pentasteron* species in Australia.

remain the main characters to define species and genera. Great care has to be taken to use appropriate characters as it now becomes clear that increase in complexity (defined as addition of apophyses and modifications) is a general phenomenon and proceeds in parallel in many, if not all spider taxa (Jocqué 1998). General characters such as 'long and flexible embolus', 'bifid embolus' should therefore be avoided. They tend to appear over and again in the course of the evolution of the palp. Appearances of new sclerites (e.g. the prolateral tegular apophysis in *Subasteron*, the basal cymbial concavity combined with the tibial concavity in *Pentasteron*) are more likely to be reliable generic discriminators. The character on which *Phenasteron* is based, the size and shape of the DTA, is less reliable because amplification of an apophysis is evidently less drastic than the addition of a new structure.

ACKNOWLEDGEMENTS

We thank M. Gray, M. Harvey, R. Raven and J. Waldoek for the loan of material. We are indebted to M. Baehr, K. Brennan and J. Shield for giving additional material, A. Reygel for his skillful habitus drawings and D. Knowles for image of *Subasteron daviesae*. We are specially grateful to R. Raven for the preparation of the distribution maps. This work was supported by the Australian

FIG. 16. Records for species of *Leptasteron*, *Phenasteron* and *Subasteron* in Australia.

Biological Resources Study Participatory Program.

LITERATURE CITED

- BAEHR, B. & JOCQUÉ, R. 1996. A revision of *Asteron* starring male palpal morphology. *Revue Suisse Zoologie*, hors série: 15-28.
2000. Revisions of genera in the *Asteron*-complex (Araneae, Zodariidae). The new genera *Cavasteron* and *Minasteron*. *Records of the Western Australian Museum* 20: 1-30.
- JOCQUÉ, R. 1991. A generic revision of the spider family Zodariidae (Araneae). *Bulletin of the American Museum of Natural History* 201: 1-160.
- 1995a. Notes on Australian Zodariidae (Araneae), I. New Taxa and Key to the Genera. *Records of the Australian Museum* 47: 117-140.
- 1995b. Notes on Australian Zodariidae (Araneae), II. Redescriptions and new records. *Records of the Australian Museum* 47: 141-160.
1998. Female choice, secondary effect of 'mate check'? A hypothesis. *Belgian Journal of Zoology* 128: 99-117.
- JOCQUÉ, R. & BAEHR, B. 2001. Revisions of genera in the *Asteron*-complex (Araneae, Zodariidae). A revision of the genus *Asteron* with description of the new genus *Pseudasteron*. *Records of the Australian Museum* 53(1): 21-36.
- LINDSEY, T. 1998. *Green guide to spiders of Australia*. (New Holland: Frenches Forest, Sydney).

A REVIEW OF *TEMNOSEWELLIA* (PLATYHELMINTHES: TEMNOCEPHALIDA) ECTOSYMBIONTS OF *CHERAX* (CRUSTACEA: PARASTACIDAE) IN AUSTRALIA

LESTER R.G. CANNON AND KIM B. SEWELL

Cannon, L.R.G. & Sewell, K.B. 2001 06 30: A review of *Temnosewellia* (Platyhelminthes) ectosymbionts of *Cherax* (Crustacea: Parastacidae) in Australia. *Memoirs of the Queensland Museum* 46(2): 385-399. Brisbane. ISSN 0079-8835.

New species are described and existing species reviewed of *Temnosewellia*, worms living ectosymbiotically on parastacid crayfish, *Cherax* spp., in Australia. □ *Temnosewellia*, *Cherax*, *Australia*, *ectosymbionts*, *crayfish*.

Lester R.G. Cannon and Kim B. Sewell, *Queensland Museum, PO Box 3300, South Brisbane 4101, Australia*; 3 June 2000.

Temnocephalida are dalyellioid rhabdocoels found as ectosymbionts, especially on freshwater crustaceans; they are characterised by a syncytial epidermis divided into a series of plates and a tendency to lose locomotory ciliation (Cannon & Joffe, 2001). Cannon (1986) recognised three families, Scutariellidae from prawns in Europe and Asia, the monotypic Actinodactylellidae from burrowing crayfish from southern Australia and the Temnocephalidae — a large and diverse family with Gondwanan associations. Sewell & Cannon (1996) resolved the position of controversial *Didymorchis*, i.e. in the Temnocephalida and within the Didymorchidae Bresslau & Reisinger, 1933. Cannon & Joffe (2001) also recognised Diceratocephalidae to include *Diceratocephala* and *Decadidymus*, each with two anterior tentacles.

By far the largest and most diverse family, Temnocephalidae, was first recorded in Australia in 1888 with *Temnocephala fasciata* Haswell, 1888 and *T. minor* Haswell, 1888 from the crayfish *Astacopsis serratus* (Shaw, 1794) and *A. bicarinatus* Gray, 1845, respectively. Today these crayfish are known to be several species, respectively in the genera *Euastacus* and *Cherax*. Haswell (1893) added temnocephalans from *A. bicarinatus* (i.e. *Cherax*), viz. *Temnocephala dendyi* Haswell, 1893 and *Craspedella spenceri* Haswell, 1893. Cannon & Sewell (1995) reviewed *Craspedella* adding new species and genera and recognising the subfamily Craspedellinae. With the exception of *Dactylocephala* from Madagascar which shows some differences (Cannon & Sewell, 2001), the remaining genera recorded within the Temnocephalidae, viz. *Temnocephala*, *Temnohaswellia*, *Temnomonticellia*, *Notodactylus*, *Achenella* and *Craniocephala* all display a similar facies and may be assigned confidently to the subfamily Temnocephalinae.

The largest genus, *Temnocephala*, has species found on a wide variety of hosts. Recently, Damborenea & Cannon (2001) reviewed members of this genus from the Neotropics and concluded that the Australian representatives should be separated as *Temnosewellia*. Here we review *Temnosewellia* from *Cherax* spp. crayfish in Australia.

Collection and processing of crayfish and worms and morphological terminology follow Cannon & Sewell (1995). All worms were highly mobile on crayfish, and unless otherwise stated, worms were recorded as collected on the surface of the crayfish exoskeleton. Several species of worms were commonly found in the branchial chamber of their crayfish hosts, but none were located there exclusively.

Recognition that the cirrus is a most effective discriminator of species has led to taxonomic descriptions that are more succinct than in previous reports (Cannon & Sewell, 1995; Sewell & Cannon, 1998). In addition, many of the specimens we examine here were collected prior to our adoption of improved techniques requiring the use of live worms, i.e. the use of de Faure's fluid to elucidate the structure of the cirrus, and the use of silver nitrate to examine the epidermal mosaic (Cannon & Sewell, 1995; Sewell & Cannon, 1998).

TERMINOLOGY AND MEASUREMENTS

Specimen data are listed in the order: QM registration number; specimen/slide preparation details (in parentheses); host scientific name; locality details; date collected; collector(s); histological fixation/staining procedures. Full registration details are provided for each holotype specimen and for each new locality. For all subsequent specimens listed in the Materials

section (including paratypes), the QM registration number and specimen/slide preparation details are provided, followed by only those data which are different from that of the preceding registration. Discrete blocks of registration data are separated by semicolons. Specimens recorded in the Materials section, other than type material, are grouped by crayfish host, then Australian State.

Unless otherwise stated, measurements provided for soft structures are taken only from the taxonomic type series and those of the cirrus from special cirrus preparations. Descriptions of the cirrus refer to the inverted state of the organ and exclude fine details of the introvert spines. All measurements were made in microns (μm) with the aid of a drawing tube. The sequence is: B, total body length to tip of tentacles \times width at greatest dimension; LE, length from posterior to eyes; SD, sucker diameter; PD, sucker peduncle diameter; PII, pharynx length \times width; LA, excretory ampullae - length \times width of left, then right, ampulla; E, diameter of left, then right, eye; AT, anterior testes - length \times width of left, then right, testis; PI, posterior testes - length \times width of left, then right, testis; S, shaft length \times width at proximal end; I, introvert length \times width.

The following other abbreviations are used:

Alc, 100% ethanol; Bouin, Bouin's fixative; CP, cirrus preparation; deF, de Faure's mounting medium; E, East; Form, 10% formalin buffered to pH 7.0 with phosphate; Form-Acetic, Acetic-Formalin-Alcohol (AFA); H, Holotype, H&E, haematoxylin & eosin stain; HF, hot 10% Formalin; HW, hot water; Hx, Mayer's or Harris's haematoxylin stain; LS, longitudinal serial sections; NSW, New South Wales; NT, Northern Territory; P, Paratype; PP, pigment preparation; QLD, Queensland; QM, Queensland Museum; S, South; WA, Western Australia; WM, wholemount.

SYSTEMATICS

Order TEMNOCEPHALIDA Family TEMNOCEPHALIDAE

Temnosewellia Damborenea & Cannon, 2001

TYPE SPECIES. *Temnosewellia minor* (Haswell, 1888) Damborenea & Cannon, 2001.

DIAGNOSIS. Temnocephalidae (Temnocephalinae) with 5 anterior tentacles, a posterior pedunculate adhesive disc, lacking conspicuous papillate ridges on tentacles or dorsal body, with dark (melanin?) pigment (if any) in body or eyes,

with 5 syncytial plates: 1, tentacular; 2, a characteristic single, saddle-like post tentacular; 3, body; 4, peduncular; and 5, adhesive disc. Furthermore, the excretory pores lie on the body plate, outside the single, post-tentacular plate.

Other Australian species from *Cherax*:

Temnosewellia acirra sp. nov.

Temnosewellia chaeropsis (Hett, 1925) Damborenea & Cannon, 2001

Temnosewellia christineae sp. nov.

Temnosewellia dendyi (Haswell, 1893) Damborenea & Cannon, 2001

Temnosewellia punctata sp. nov.

Temnosewellia phantasmella sp. nov.

KEY TO SPECIES OF *TEMNOSEWELLIA* FROM AUSTRALIAN *CHERAX* SPP. CRAYFISH:

1. Lacking pigment except for eyes 2
Dark pigment tracery on dorsal, and sometimes ventral, surface 3
2. Lacking any male sclerotic copulatory apparatus
T. acirra sp. nov.
With sclerotic male copulatory apparatus bearing 1 or more large sharp spines at the base of the introvert
T. dendyi
3. Dense even pigment in blocks emphasising neural net, without posterior marginal glands
T. christineae sp. nov.
Dorsal pigment a tracery, with posterior marginal glands 4
4. Marginal glands posterolateral only, front eastern Australia 5
Marginal glands posterior, from WA 6
5. Pigment an open tracery, extending to tentacles; cirrus curved
T. minor
Pigment very open, concentrated about excretory pores, not extending to tentacles; cirrus short and conical
T. phantasmella sp. nov.
6. Pigment decidedly clumped, most noticeable on body periphery and tentacles, several small glands along posterior body margin
T. punctata sp. nov.
Pigment a dense tracery, two prominent, adjacent glands at posterior extremity of body
T. chaeropsis

Temnosewellia acirra sp. nov. (Figs 1, 2)

Temnocephala sp. 2: Joffe & Cannon, 1998:3.

ETYMOLOGY. Latin, lacking a cirrus.

MATERIAL. HOLOTYPE: QMGL18689 (WM), ex *Cherax destructor*, dam, Eukey Qld (28°46.2'S 151°59.2'E) 18/Apr/1990, S.D. Cook, Form/Hx. PARATYPES: QMGL18690-18691 (WM); QMGL18693 (LS[1]), Condamine R., Warwick Qld (28°11.4'S 151°57.5'E) 24/Oct/1992, K.B. & S.G. Sewell, Bouin/H&E; QMGL18702 (LS[2]), ex *Cherax destructor*, Bungil Ck, Roma (26°30'S 148°48'E) 2/Dec/1991, L.R.G. Cannon & J.B. Jennings, Form/Hx; QMGL18710 (LS[3]),

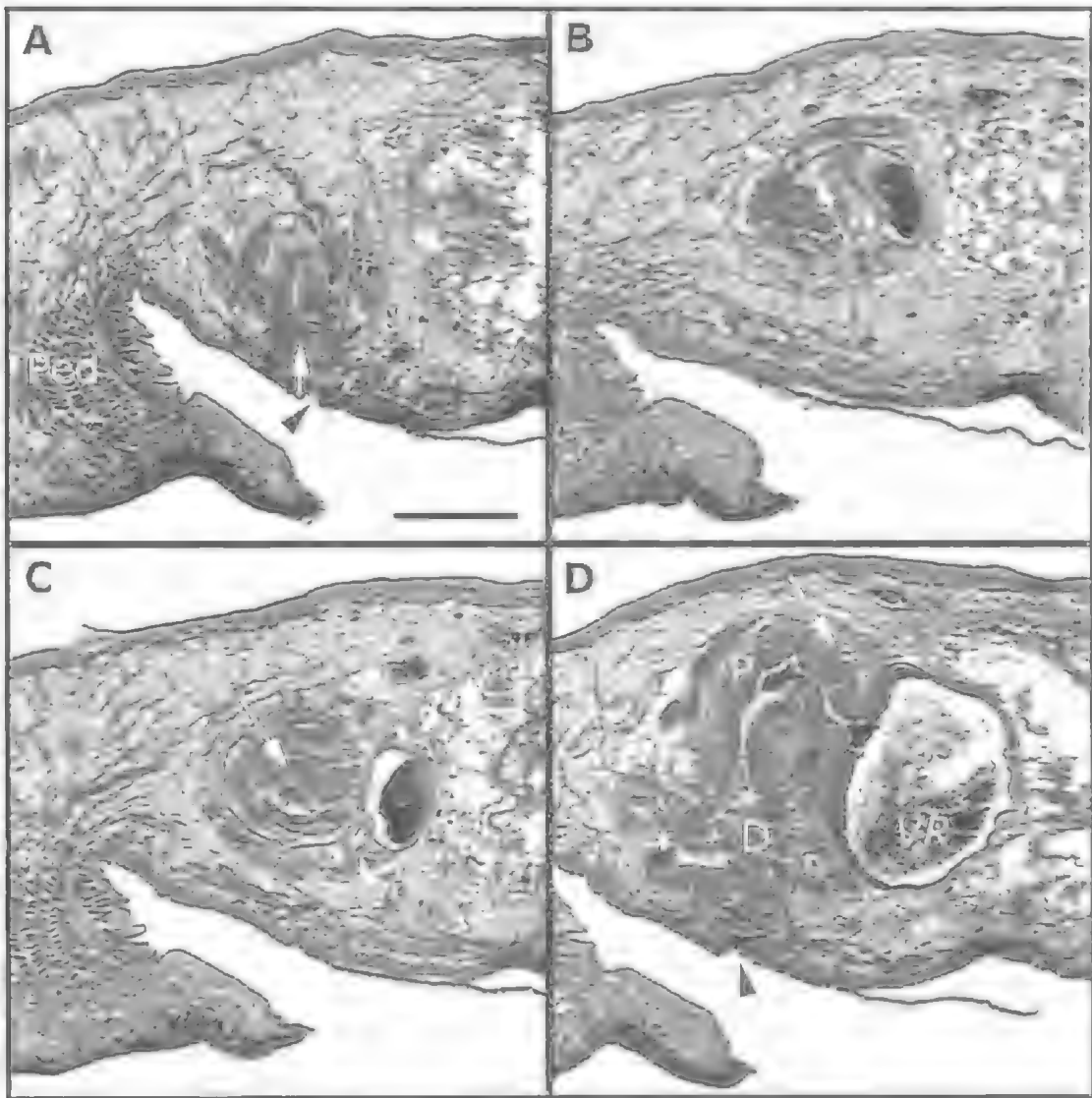


FIG. 1. *Temnosewellia acirra*. Longitudinal section through genital region of QMGL18710. A-C, ♂. D, ♀. A, gonopore (arrow head), distal muscular 'penis' (arrow) and peduncle (Ped). B, junction of ejaculatory sac (arrowhead) with proximal copulatory bulb dorsal to the distal seminal vesicle junction (arrow). C, vas deferens (arrowhead) entering proximal seminal vesicle adjacent to copulatory bulb (arrow). D, from vesicula resorbens (VR) to gonopore (arrowhead). A muscular duct connects the vesicula resorbens to the proximal vagina (P) where the vitelline duct (arrow) enters. The proximal vagina is more muscular than the distal vagina (D) which opens to the common atrium and blind caecum or copulatory bursa (*). Scale = 100µm.

12km SSE of Armidale (30°31'S 51°40'E) 26/Feb/1987, W. Higgins Form/H&E.

OTHER MATERIAL. Ex *Cherax destructor*. QLD: QMGL18711 (WM), Marlong Ck, Mt Moffat Nat. Pk (25°02'S 147°54'E), 26/Feb/1986, N.C. Monteith, 70% Alc/Hx; QMGL18703-18705 (WM), Willows gemfield, in dam beside road near Emerald (23°45'S 147°25'E 20/Oct/1990, S.D. Cook, HW/Form/Hx; QMGL18706

(LS[5]), HW/Form/H&E; QMGL18700-18701 (WM), Bungil Ck, Roma (26°30'S 148°48'E) 2/Dec/1991, L.R.G. Cannon & J.B. Jennings, Form/Hx; QMGL18695-18699 (WM), dam, Eukey (28°46.2'S 151°59.2'E) 18/Apr/1990, S.D. Cook, Form/Hx; QMGL18692 (LS[2]), HW/Form/H&E, same locality. NSW: QMGL18707-18708 (WM), 12km SSE of Armidale (30°31'S 51°40'E) 26/Feb/1987, W. Higgins Form/Hx; QMGL18709 (LS[3]), Form/H&E.

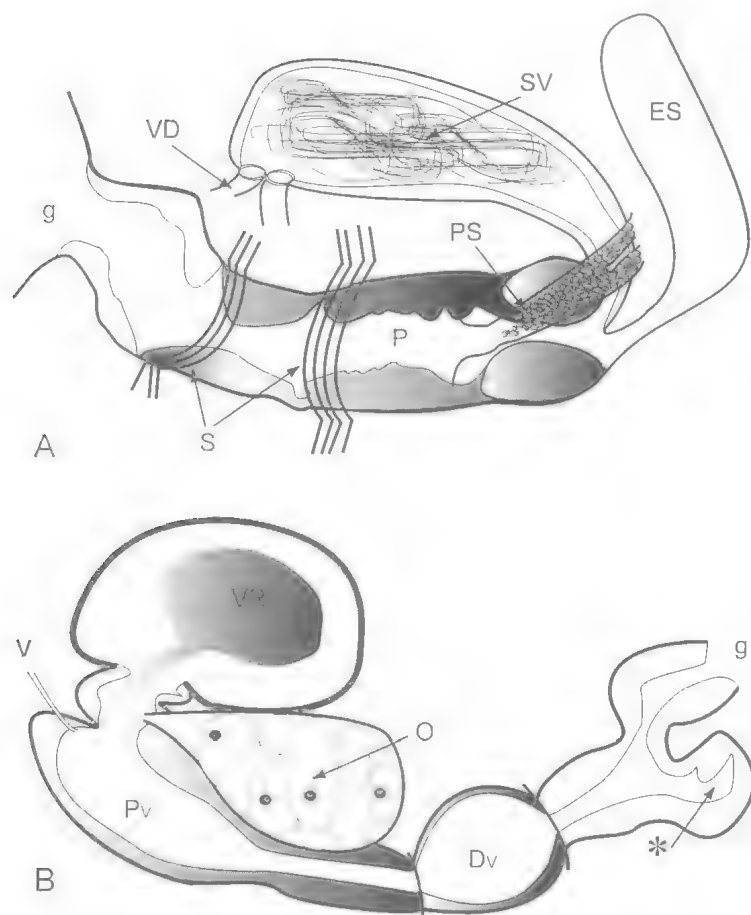


FIG. 2. *Temnosewellia acirra* copulatory structures. A, ♂; B, ♀. ES, ejaculatory sac; g, gonopore; P, muscular 'penis'; PS, prostate secretions; S, sphincter; SV, seminal vesicle; VD, vas deferens.

DESCRIPTION. *General Anatomy.* A medium sized, rather thick-bodied worm without body pigment except for two eyespots set close together. A small cluster of posterolateral glands present. Selected measurements are: QMGL18689 (H): B(1675×1041), LE(1302), SD(651), PD(385), PH(183×426), EA(89×59 & 89×59), ED(47 & 47); AT(266×219 & 296×237), PT(278×278 & 314×260); QMGL18690 (P): B(1858×1000), LE(1479), SD(657), PD(396); PH(195×473), EA(95×65 & 89×59), ED(41 & 41); AT(302×207 & 290×201), PT(284×284 & 308×266); QMGL18691 (P): B(1728×1087), LE(1361), SD(521), PD(308); PH(237×343), EA(101×77 & 112×71), ED(41 & 41); AT(225×148 & 278×178), PT(278×219 & 272×237).

Reproductive System. Female. No seminal receptacles, but a globular muscular duct lies

between the vesicula resorbens and the top of the muscular vagina; vagina has a large proximal chamber and a smaller distal chamber with ridged walls, this opens via a sphincter into a female antrum which in turn passes to the common genital atrium which is voluminous and opens also to a caecum (bursa copulatrix).

Male. Testes with several large lobes when fully mature, anterior testis lies laterally at mid gut level, posterior testis at level of posterior of gut, seminal vesicle relatively thin walled, ejaculatory sac only slightly smaller, copulatory bulb, prostate without large reservoirs, totally lacking any sclerotic armature of male organ which consists of a muscular tube lined with a high epidermis; at the distal end is a sphincter and the duct opens to a large male antrum also lined with a high epidermis, a second sphincter lies at the mouth to the common genital atrium.

HOST. *Cherax destructor* (Parastacidae).

LOCALITY. Known from tributaries of the Murray Darling system draining westward from Armidale in central NSW north to the Carnarvon region of central Queensland.

REMARKS. This is the only species to lack a sclerotic stylus or cirrus. In some sections the muscular proximal tube is seen to push or evert into the male antrum and thus assume the role of a penis. Another unusual feature is the large bursa copulatrix or caecum opening from the common atrium. This worm lives in the branchial chamber, or nearby sheltered body regions, of *C. destructor* and alongside *Temnosewellia dendyi* which it superficially resembles in size and lack of pigment. *T. dendyi* has the following characters which serve to distinguish it from the new species: the pharynx is smaller, the posterior testis is set further back behind the gut and it has, apart from a prominent cirrus armed with a

distinctive central stylet, a longer and more muscular copulatory bulb in which prostate vesicles are aligned along the duct, and a muscular ejaculatory sac, which is not reflexed, opening via a wide mouth at the back of the copulatory bulb. In the female, there are 3-4 seminal receptacles. Furthermore, the rhabdite glands are fewer and larger.

Joffe & Cannon (1998: fig. 3E,J) identified and figured the epidermal mosaic of worms they identified as *Temnocephala* sp. 2 ex *Cherax destructor* from the Condamine R., Warwick. We can now formally identify these worms as *Temnosewellia acirra*.

***Temnosewellia chaeropsis* (Hett, 1925)**

Damborenea & Cannon, 2001

(Figs 3A,H, 5A, 6A)

Temnocephala chaeropsis Hett, 1925:569.

MATERIAL. Ex *Cherax tenuimanus*. WA: QMGL18717-18722 (WM), Inlet R., on South Western Highway to Walpole (34°55.2'S 116°34.2'E) 25/Jan/1992, L.R.G. Cannon & K.B. Sewell, HW/Form/Hx; QMG18716 (LS[1]); QMG217457 (CP), HW/Form/deF; QMG217499-217500 (CP); QMG217502 (CP); QMG217458 (PP); QMG217501 (PP); QMG217503 (PP).

Ex *Cherax* cf. *quinquecarinatus*. WA: QMGL18712-18715 (LS[1 each]), Inlet R., on South Western Highway to Walpole (34°55.2'S 116°34.2'E) 25/Jan/1992, L.R.G. Cannon & K.B. Sewell, HW/Form/H&E.

DESCRIPTION. *General Anatomy.* As described by Hett (1925), but with a fine tracery of pigment dorsally, becoming much less dense ventrally.

Reproductive System. Female. The female reproductive system has a distinctly bipartite vagina: distally globose and strongly muscular with a powerful distal sphincter, proximally narrow, with distinct seminal receptacles as described by Hett (1925, text-fig. 7).

Male. The cirrus is slightly curved (Fig. 5A), with a small, inconspicuous ejaculatory sac. Posterior gland reservoirs often contiguous (Fig. 3H). Selected measurements are: QMG217457: S(186×75); I(50×31); QMG217499: S(166×62), I(52×24); QMG217500: S(182×80), I(?×25); QMG217502: S(154×78), I(52×30).

HOSTS. *Cherax tenuimanus*, *C. cf. quinquecarinatus* (Parastacidae)

LOCALITY. Southwestern WA.

REMARKS. Originally known only from some preserved specimens conveyed to England. No types were designated, but the characteristic

posterior gland reservoirs as two adjacent bulbs are quite distinctive. Hett (1925) said of *T. chaeropsis* that the entire animal showed no evidence of pigment (although they had been 'for some time in spirit'), but in sections dorsal pigment cells were apparent. Pigment is really quite extensive particularly dorsally. Furthermore, she said 'the penis, which is straight, has no terminal dilation', in fact the cirrus does curve slightly, though the introvert is hardly wider than the distal shaft. She claimed also 'there is no distinct ejaculatory sac': it is true that this sac is quite small and indistinct. Hett further remarked on the presence of seminal receptacles which she considered unique; in fact, Merton (1913) had described such structures from *Temnocephala rouxi*.

Hett (1925) commented extensively on the paired posterior glandular organs which she believed the distal ends of rhabdite glands (cf Hett, 1925, text-fig. 8 with Fig. 3H). Until Cannon (1993) and Cannon & Sewell (1995) described similar structures from other temnocephalans, *T. chaeropsis* was considered unique in having such glands. This led Cannon to incorrectly identify worms which were taken from WA marron, *Cherax tenuimanus*, cultured in South Africa, as *T. chaeropsis*. It has now been established that such glands are also found in *T. minor*, but have been overlooked (Cannon & Watson, 1996). Reports of *T. chaeropsis* from cultured marron in South Africa (Mitchell & Kok, 1988; Avenant-Oldewage, 1993) are incorrect: the worms are *T. minor*.

***Temnosewellia christineae* sp. nov.**

(Figs 3B, 5B, 6B)

ETYMOLOGY. In memory of Dr Christine Cannon.

MATERIAL. HOLOTYPE: QMGL18901 (WM), ex *Cherax depressus*, Gap Ck, Gap Ck Reserve picnic ground, Brookfield, Qld (27°28.7'S 152°55.7'E) Nov/1984, L.R.G. Cannon, AFA/Hx. PARATYPE: QMGL18902 (LS[7]); QMGL18903 (WM), 3/Sep/1984; Bouin/H&E.

OTHER MATERIAL. Ex *Cherax depressus*. QLD: QMGL18904-18905 (WM), Gold Coast (28°00'S 153°25'E), Dec/1983, L.R.G. Cannon, Form/Hx; QMGL18906-18907 (LS[3,3]), Bouin/H&E; QMGL18908-18918 (WM), gully near Capalaba (27°32'S 153°12'E) 22/Sep/1988, L.R.G. Cannon, AFA/Mayer's; QMGL18919-18921 (WM), Bouin/Hx; QMGL18922-18928 (LS[3,4,7,5,4,7,4]), Bouin/Hx; QMGL18929-18930 (WM), 19/Sep/1988, Alc/Hx; QMGL18931-18932 (WM), Winston Ck Rd, Sheldon (27°34'S 153°12'E), 18/Mar/1990; I. Forrester & L.R.G. Cannon, Form/Hx; QMGL18933 (LS[5]), Bouin/H&E;

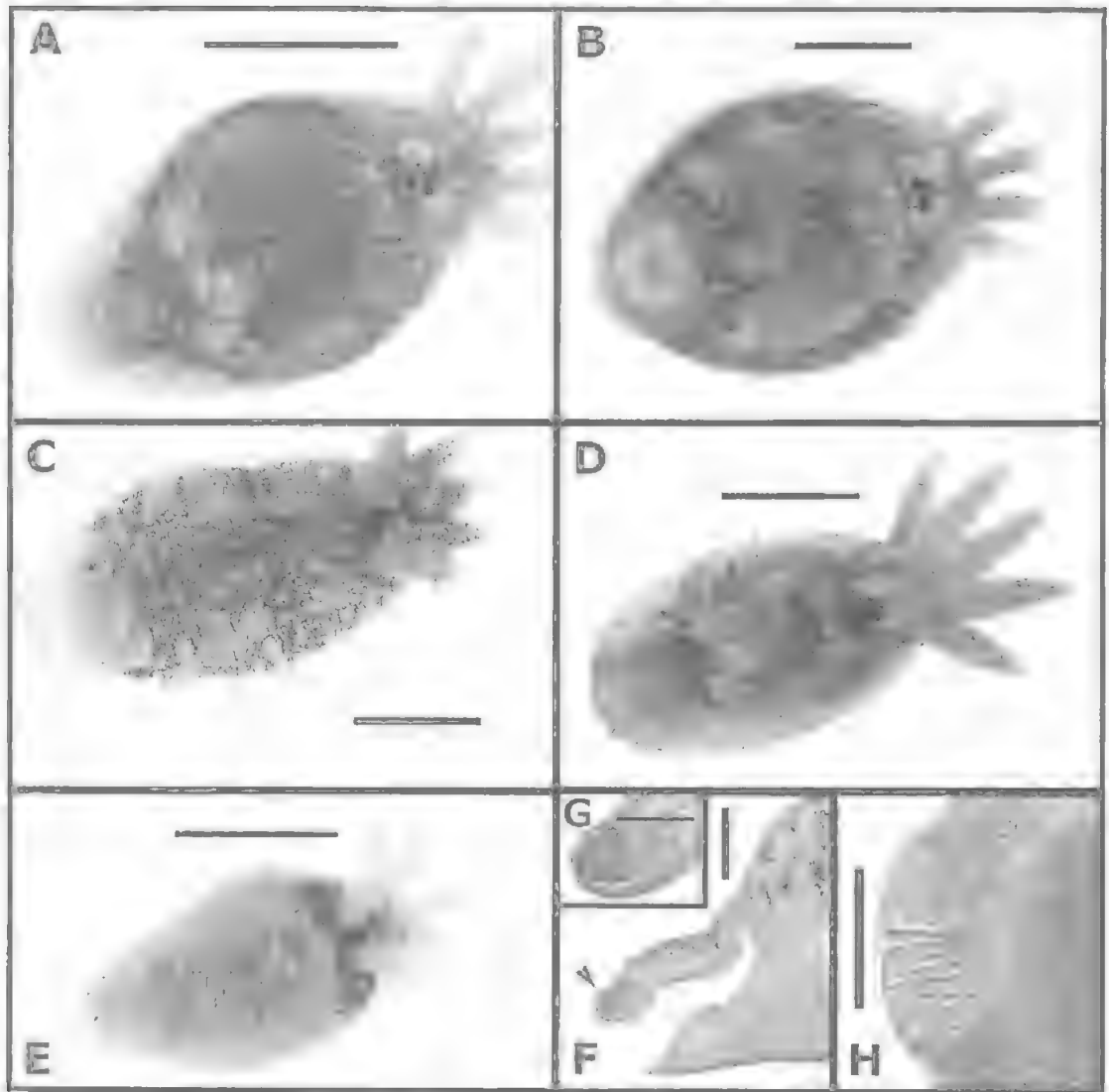


FIG. 3. *Temnosewellia* species showing pigment patterns (scales A-E = 500 µm) and posterior glands (scales F and H = 100 µm, scale G = 50 µm). A, *T. chaeropsis* QMG217458; B, *T. christineae* QMG217467; C, *T. minor* QMGL18876; D, *T. punctatus* QMG217471; E, *T. phantasmella* QMG217477; F, G, *T. punctatus* QMGL18861; H, *T. chaeropsis* QMG217458.

QMGL18934-18937 (WM), Wallaby Ck, on Henderson Rd 0.2km from Mt Cotton Rd junction, Sheldon (27°34.2'S 153°12.8'E) 18/Mar/1990; L.R.G. Cannon, Form/Hx; QMGL18938-18939 (LS[9,7]), Bouin/H&E; QMGL18940-18941 (WM), Gap Ck, Gap Ck Reserve picnic ground, Brookfield (27°28.7'S;152°55.7'E) Nov/1984, L.R.G. Cannon, AFA/Hx; QMGL18942 (WM), 2/Apr/1984, N. Hall; QMGL18943 (WM), Nov/1985, J. Jennings; QMGL18944-18945 (WM), Ithaca Ck (27°29'S;152°57'E) 22/Oct/1988, J. Short & L.R.G. Cannon, AFA/Hx; QMGL18946 (LS[5]), Bouin/H&E; QMGL18947-18948 (WM), gully on Mumford Rd,

Narangba (27°12.1'S 152°57.3'E), 22/Apr/1990, J. Short & L.R.G. Cannon, AFA/Hx; QMGL18949 (LS[9]), Bouin/H&E; QMG217459-217463 (CP), creek down stream from Kelly St crossing, Narangba (27°12'S 152°57'E) 19/Oct/1997, J.W. Short, HW/def; QMG217464-217467 (PP); QMGL18950-18951 (WM), Kroombit Ck, trib TA64 (24°22.9'S 150°59.8'E) 19/Sep/1990, L.R.G. Cannon & K.B. Sewell, HW/AFA/Hx; QMGL18952-18953 (LS[4,6]), Kroombit Ck, trib TA47 (24°22.2'S;150°58.5'E), 20/Sep/1990, L.R.G. Cannon & K.B. Sewell, Bouin/H&E; QMGL18954-18955 (WM), 20/Sep/1990, HW/AFA/Hx;

QMGL18956-18960 (WM), Kroombit Ck, Beauty Spot 98 (24°23'S 150°59'E), 21/Sep/1990; QMGL18961-18962 (LS[4,3]).

Ex *Cherax robustus*. QLD: QMGL18877-18878 (WM), Sunshine Ck, Sunshine Beach (26°24.5'S 153°06.5'E) 16/Apr/1990, J.W. Short & L.R.G. Cannon, AFA/Hx; QMGL18880 (WM); QMGL18882 (WM); QMGL18879 (LS[20]); QMGL18881 (LS[2]); QMGL18883-18885 (LS[8,2,2]), Bouin/H&E.

DESCRIPTION. *General Anatomy.* A medium sized worm with a distinctive pigment pattern dorsally appearing as a series of blocks emphasising the neural network. Selected measurements are: QMGL18901 (H): B(3650 × 1635), LE(2336), SD(633), PD(314); PH(521 × 432), EA(207 × 112 & 230 × 112), ED(65 & 65); AT(432 × 284 & 432 × 161), PT(336 × 263 & 373 × 260); QMGL18903 (P): B(1796 × 1460), LE(1460), SD(509), PD(314); PH(350 × 321), EA(201 × 160 & 189 × 142), ED(65 & 77); AT(260 × 166 & 272 × 160), PT(284 × 172 & 337 × 172).

Reproductive System. Female. The vesicula resorbens leads through a short tube and is joined by the ovary, four small seminal receptacles and the vitelline duct before opening to a muscular vagina with a prominent distal sphincter at the entrance to a commodious common atrium.

Male. Swollen vasa deferentia enter separately a seminal vesicle so reduced as to resemble no more than a thickened ejaculatory canal. It and the ejaculatory sac, which is large, enter the base of the cirrus side by side together with the prostate gland ducts: there is no obvious copulatory bulb. Selected measurements are: QMG217459: S(468 × 86); I(77 × 31); QMG217460: S(337 × 59), I(75 × 30); QMG217461: S(465 × 80), I(77 × 32); QMG217462: S(468 × 145), I(75 × 28); QMG217463: S(479 × 109), I(74 × 30).

HOSTS. *Cherax depressus* and *C. robustus* (Parastacidae).

LOCALITY. Known from SEQ and Kroombit Tops CEQ.

REMARKS. Potentially confused with *T. minor*, but the pigment pattern is much more regular. This pattern is reminiscent of that illustrated by Haswell (1893) of a young *T. fasciata* (Haswell, 1888) from crayfish now recognised as *Euastacus* spp. Furthermore, the cirrus of *T. christineae* is at least twice as long with a more oval introvert when inverted than that of *T. minor*. This cirrus is not dissimilar to that illustrated by Haswell (1893: pl. XIII, fig. 14) as a variant of *T.*

fasciata, though we now know that a great diversity of worms occur on these crayfish (Cannon & Sewell, 1994).

Small and large specimens of this worm swim using rapid dorso-ventral movements of the body and tentacles: it is the only temnocephalan known to swim.

***Temnosewellia dendyi* (Haswell, 1893)
Damborenea & Cannon, 2001
(Figs 5C, 6C)**

Temnocephala dendyi Haswell, 1893:135.

MATERIAL. Ex *Cherax albidus*. VIC:QMGL18748 (WM), creek on Mathison Rd, 6km S of Winchelsea (38°15'S 143°59'E), 30/Sep/1991, L.R.G. Cannon & K.B. Sewell, HW/Form/Hx; QMGL18749 (LS[2]), HW/Form/H&E.

Ex *Cherax destructor*. QLD: QMGL18723-18724 (WM), Bungil Ck, Roma (26°30'S 148°48'E) 3/Dec/1986, L.R.G. Cannon & J.B. Jennings, Form/Hx; QMGL18725-18727 (LS [5,6,8]), AFA/H&E; QMGL18728-18729 (WM), 2/Dec/1986; QMGL18730 (LS[2]), AFA/H&E; QMGL18731 (WM), Western R. 1.5km from Winton on Jundah Rd. (22°24.2'S 143°02.2'E) 22/Sep/1990, S.D. Cook, 70% Alc/Hx; QMGL18732 (LS[4]), Willows gemfield in dam beside road (23°45'S 147°25'E) 20/Sep/1990, S.D. Cook, 70% Alc/H&E; QMGL18733 (WM), dam at Eukey (28°46.2'S 151°59.2'E) 18/Apr/1990, S.D. Cook, 70% Alc/Hx; QMGL18734-18736 (WM), Accommodation Ck, near Bald Mountain (28°52.9'S 151°53.7'E) 10/Apr/1990, L.R.G. Cannon & K.B. Sewell, HW/AFA/Hx; QMGL18737 (LS[3]), HW/AFA/H&E; QMGL18738-18740 (LS[1,1,1]), Condamine R., Warwick (28°11.4'S 151°57.5'E) 24/Oct/1992, K.B. & S.G. Sewell, Bouin/H&E; QMG217489-217493 (CP), 4/Aug/1994, K.B. Sewell & B.I. Joffe HW/deF; QMG217494-217495 (CP), 25/Jun/1996, K.B. Sewell, R.D. Adlard & R.D. Sewell; QMGL18900 (WM), creek by Marlborough Caravan Park, Marlborough (22°49.2'S 149°53.2'E), L.R.G. Cannon & K.B. Sewell, 20/Sep/1990, HW/AFA/Hx. NSW: QMGL18741-18743 (WM), Lake Madgwick, UNE campus, Armidale (30°31'S 151°40'E) 23/May/1991, Zoology Dept. UNE, Bouin/Hx; QMGL18744 (LS[3]), Yarunga Ck tributary, 1.2km NW Fitzroy Falls Morton NP. (34°38.4'S 150°28.4'E) 19/Oct/1991, L.R.G. Cannon & K.B. Sewell, Bouin/H&E. SA: QMGL18750-18751 (WM), Kangaroo I. (35°50'S 137°15'E) 11/Aug/1995, S. Nichols, Form/Hx; QMGL18752 (WM), Coopers Ck (27°44'S 140°15'E) 26/Nov/1988, I. Beveridge, Form-Acetic/Hx; QMGL18753 (WM), Bool Lagoon (37°09'S 140°43'E) 15/Nov/1988, I. Beveridge, Form-Acetic/Hx; QMGL18754 (WM), Mt Jagged, 9/Feb/1988, I. Beveridge, Form-Acetic/Hx; QMGL18755 (WM), Lake Merretti (34°01'S 140°46'E), 3/Dec/1988, I. Beveridge, Form-Acetic/Hx; QMGL18756 (WM), The Narrows via Clayton (29°17'S 138°23'E), 2/Dec/1988, I. Beveridge, Form-Acetic/Hx; QMGL18757-18758 (WM), Mt Benson

((37°02'S 139°49'E) 18/Oct/1988, I. Beveridge, Form-Acetic/Hx; QMGL18759 (WM), Lake Alexandrina (35°25'S 139°10'E) 20/Jan/1989, I. Beveridge, Form-Acetic/Hx; QMGL18760 (WM), Bordertown (36°18'S 140°46'E) 31/Oct/1988, I. Beveridge, Form-Acetic/Hx. VIC: QMGL18745-18746 (WM), creek on road to Ballan 15km S of Daylesford (37°21'S 144°09'E) 6/Oct/1991, L.R.G. Cannon & K.B. Sewell, HW/Form/Hx; QMGL18747 (LS[2]), HW/Form/H&E. Ex *Cherax robustus*. QLD: QMG217496, G218301 (CP), trackside pond on McMahon Rd, Bribie I. (27°02.5'S 153°10.3'E) 31/Jan/1995, K.B. Sewell, L.R.G. Cannon, Z. Kalil & J. Short HW/deF. Ex *Cherax depressus*. QLD: QMG217487-88 (CP), Wallaby Ck, Sheldon, 27/Sep/1994, K.B. Sewell, B.I. Joffe, I. Solovei & S. Solovei, HW/deF.

DESCRIPTION. *General Anatomy.* Largely as described by Haswell (1893). Moderately large and without pigment except for the eyes.

Reproductive System. Female. Vesicular resorbens opening to duct into which open 4 seminal receptacles along with ovary and vitelline duct. Vagina reflexed proximally, muscular with distal sphincter. Common atrium large with a small posterior caecum (bursa copulatrix).

Male. The vasa deferentia enter the seminal vesicle separately; the seminal vesicle has narrow distal region surrounded by massed prostate glands which enter the base of the copulatory bulb, their ducts continuing parallel to the ejaculatory duct. Selected measurements are: ex *Cherax depressus*, QMG217487: S(194 × 75), I(93 × 19); QMG217488: S(158 × 95), I(93 × 22); QMG217489: S(260 × 118), I(101 × 27); QMG217490: S(182 × 62), I(96 × 25); QMG217491: S(274 × 139), I(101 × 27); QMG217492: S(271 × 104), I(92 × 21); QMG217493: S(259 × 96), I(95 × 22); QMG217494: S(243 × 98), I(90 × 18); QMG217495: S(158 × 52), I(98 × 19); ex *Cherax robustus* QMG217496: S(192 × 58), I(99 × 19); QMG217497: S(183 × 75), I(99 × 24).

HOST. *Cherax destructor*, *C. albidus* and *C. robustus* (Parastacidae).

LOCALITY. Known from the Murray-Darling system in Qld., NSW, Vic. and SA, but also from coastal Qld and Kangaroo Is.

REMARKS. This and *T. acirra* may co-inhabit the branchial chamber and nearby protected locations on the principal host, *Cherax destructor*. The worms are of similar size and since both lack pigment can be superficially confused (see remarks on *T. acirra* above). The details of the cirrus of specimens from different hosts and from widely separated regions are very

similar (Figs 5C, 6C show the cirri of worms from *Cherax depressus* and *C. robustus* are indistinguishable from those from *C. destructor* well illustrated by Haswell (1893: pl. 12, fig. 7).

The pattern of the mosaic of *T. dendyi* ex *Cherax destructor* from the Condamine R. Warwick was described and figured by Joffe & Cannon (1998: figs 2J; 4A-C).

Joffe & Cannon (1998) identified worms close to *T. dendyi* from *Cherax dispar* and *C. depressus* from Wallaby Creek, Sheldon and described the epidermal mosaic as identical to that of *T. dendyi*: these worms were *T. dendyi* (Fig. 5Ci).

***Temnosewellia minor* (Haswell, 1888)**
Damborenea & Cannon, 2001
(Figs 3C, 4, 5D, 6D)

Temnocephala minor Haswell, 1888:284; Haswell, 1893:134.

MATERIAL. Ex *Cherax albidus*. SOUTH AFRICA: QMGL18854-18855 (WM) between Dardanap and Lowden on Patterson Rd (in culture), 6/Sep/1991, H.J. Schoonbee, Form/Hx; QMGL18856 (LS[2]) Form/H&E. Ex *Cherax depressus*. QLD: QMGL18963-18966 (WM), Gold Coast, (28°00'S 153°25'E), Dec/1983, L.R.G. Cannon, Form/Hx; QMGL18967-18968 (LS[2,2]), Form/H&E; QMGL18969 (WM), gully near Capalaba, (27°32'S 153°12'E) 22/Sep/1988, L.R.G. Cannon, AFA/Hx; QMGL18970-18972 (WM), Bouin/Hx; QMGL18973-18975 (LS[1,2,3]), Form/H&E; QMGL18976-18977, 18985-18988 (WM), Wallaby Ck., on Henderson Rd 0.2km from Mt Cotton Rd junction, Sheldon (27°34.2'S 153°12.8'E) 18/Mar/1990, I. Forrester & L.R.G. Cannon, Form/Hx; QMGL18983 (WM), AFA/Hx; QMGL18984 (WM), Bouin/Hx; QMGL18978-18982 (LS[2,3,3,3]), Form/H&E; QMG217478-217479 (CP) 22/Sep/1994, K.B. Sewell, B.I. Joffe & I.V. & S. Solovei, HW/deF; QMGL18989 (LS[3]), Winston Rd, Sheldon (27°34'S 153°12'E) 18/Mar/1990, I. Forrester & L.R.G. Cannon, AFA/H&E; QMGL18990 (WM) Gap Ck, Gap Ck Reserve picnic ground, Brookfield, (27°28.7'S 152°55.7'E) Nov/1984, J. Jennings, Form/Hx; QMGL18991 (LS[2]), Form/H&E; QMGL18992 (WM), creek by Marlborough Caravan Park, Marlborough (22°49.2'S 149°53.2'E), L.R.G. Cannon & K.B. Sewell, 20/Sep/1990, Form/Hx. Ex *Cherax destructor*. QLD: QMGL18762-18763 (LS[2,2]), Western R., 1.5km from Winton on Jundah Rd (22°24.2'S 143°02.2'E) 22/Sep/1990, S.D. Cook, 70% Alc/H&E; QMGL18764 (LS[1]), Thompson R. at Longreach waterhole. (23°24.7'S 144°13.8'E) 2/Oct/1990, L.R.G. Cannon & K.B. Sewell, HW/Form/H&E; QMGL18765-18767 (WM), in dam beside road, Willows gemfield (23°45'S 147°25'E) 20/Sep/1990, S.D. Cook, 70% Alc/Hx; QMGL18768-18770 (LS[1,2,2]), 70% Alc/H&E; QMGL18771 (WM), Marlong Ck, Mt Moffat NP (25°02'S 147°54'E), 26/Sep/1986, N.C. Monteith, 70% Alc/Hx; QMGL18772 (LS[4]), 70% Alc/H&E; QMGL18773 (WM), Dawson R. Taroom (25°39'S 149°48'E) 3/Dec/1986, L.R.G. Cannon

& J.B. Jennings, Form/Hx; QMGL18774 (LS[3]), Form/H&E; QMGL18775-18777 (WM), Bungil Ck. Roma (26°30'S 148°48'E), 2/Dec/1991, L.R.G. Cannon & J.B. Jennings, Form/Hx; QMGL18780-18781 (LS[2,2]), Form/H&E; QMGL18778-18779 (LS[2,3]), 3/Dec/1991, Bouin/H&E; QMGL18782 (WM), Wilson R. at Noccundra, W of Thargomindah (27°49'S 142°35'E) 17/Apr/1990, G.B. Monteith, 70% Alc/Hx; QMGL18783-18784 (LS[1,1]), Condamine R., Warwick (28°11.4'S 151°57.5'E) 24/Oct/1992, K.B. Sewell & S.G. Sewell, Bouin/H&E; QMGL18785-18786 (WM), Feb-Mar/1993, L.R.G. Cannon, silver nitrate; QMG217481-217482 (CP), 4/Aug/1994, Sewell & B.I. Joffe, HW/deF; QMG217483 (CP) 1/Sep/1994, K.B. Sewell; QMG217484 (CP) 25/Jun/1996, K.B. Sewell; R.D. Adlard & R.D. Sewell; QMG217485-217486 (PP); QMGL18787-18788 (WM), dam at Eukey (28°46.2S 151°59.2'E) 17/Apr/1990, S.D. Cook, 70% Alc/Hx; QMGL18789-18791 (LS[4,3,3]), 70% Alc/H&E. NSW: QMGL18804 (WM), Lake Madgwick, UNE campus, Armidale (30°31'S 151°40'E), 26/Feb/1987, W. Higgins, Bouin/Hx; QMGL18805-18807 (WM) 23/May/1991, Zoology Dept. UNE; QMGL18808 (LS[4]), Bouin/H&E; QMGL18809-18811 (WM), Yarunga Ck trib., 1.2km NW Fitzroy Falls Morton NP. (34°38.4'S 150°28.4'E), 19/Oct/1991, L.R.G. Cannon & K.B. Sewell, HW/Form/Hx; QMGL18812-18813 (LS[4,3]), Bouin/H&E; QMGL18814-18818 (WM), trib. of Murrumbidgee R. on Nanangro Rd, near Childowah, outside Yass (34°51'S 148°55'E), 16/Oct/1991, L.R.G. Cannon & K.B. Sewell, HW/Form/Hx; QMGL18819 (LS[3]), HW/Form/H&E. VIC: QMGL18820 (WM), creek on Mathison Rd. 6km S of Winchelsea (38°15'S 143°59'E) 30/Sep/1991, L.R.G. Cannon & K.B. Sewell, HW/Form/Hx; QMGL18821 (LS[3]), HW/Form/H&E. SA: QMGL18822 (WM), Cowell (33°41'S 136°55'E) 8/Dec/1988, I. Beveridge, Form-Acetic/Hx; QMGL18823 (WM), Lake Merreti (34°01'S 140°46'E), 3/Dec/1988; QMGL18824 (WM), Avenue Ra. (37°05'S 140°18'E), 18/Oct/1988; QMGL18825 (WM), Onkaparinga R. (35°00'S 138°49'E) 22/Feb/1988; QMGL18826 (WM), Murray R., Murray Bridge (35°07'S 139°16'E) 10/Feb/1989; QMGL18827 (WM), Lake Alexandrina (35°25'S 139°10'E) 20/Jun/1989; QMGL18828 (WM), Inman R. (35°30'S 138°31'E) 19/Nov/1988; QMGL18829 (WM), Bordertown (26°18'S 140°46'E) 31/Oct/1988; QMGL18830-18831 (WM), Mt Benson (37°02'S 139°49'E), 18/Oct/1988; QMGL18832 (WM), Bool Lagoon (37°09'S 140°43'E), 15/Nov/1988.

Ex *Cherax dispar*: QLD: QMG217480 (CP) Wallaby Ck, on Henderson Rd, 0.2km from Mt Cotton Rd junction, Sheldon (27°34.2'S 153°12.8'E) 22/Sep/1994, K.B. Sewell, B.I. Joffe & I.V. & S. Solovei HW/deF; QMGL18792-18794 (WM), Woodgate Lagoons (25°07.4'S 152°30.6'E) 6/Apr/1991, K.B. Sewell, Form/Hx; QMGL18795 (WM) 18/Sep/1990, L.R.G. Cannon & K.B. Sewell, Form/Hx; QMGL18796 (WM), Form/unstained.

Ex *Cherax quadricarinatus*: QLD: QMGL18761 (WM), Deception Bay (in culture) (27°10'S 153°05'E)

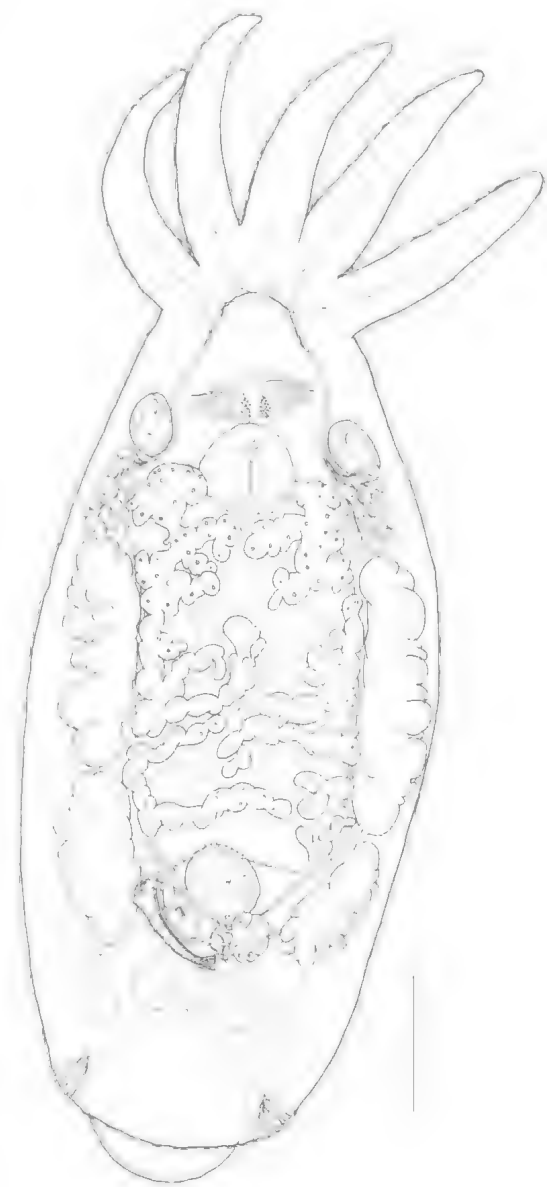


FIG. 4. *Temnosewellia minor*. Scale = 500µm.

22/Oct/1986, B. Herbert, Form/Hx.

Ex *Cherax tenuimanus*: QLD: QMGL18797-18801 (WM), Ipswich (in culture) (27°37'S 152°47'E) 12/Oct/1982, L.R.G. Cannon, Form/Hx; QMGL18802-18803 (WM), Esk (in culture) (27°14'S 152°25'E) 28/Sep/1982, L.R.G. Cannon, Form/Hx. SA: QMGL18833 (WM), Parilla (in culture) (35°18'S 140°40'E) 11/Oct/1988, I. Beveridge, Form-Acetic/Hx. WA: QMGL18834 (WM), Inlet R., SW hwy. to Walpole (34°55.2'S 116°34.2'E) 25/Jun/1992, L.R.G. Cannon & K.B. Sewell, HW/Form/Hx; QMGL18835-18836 (WM),

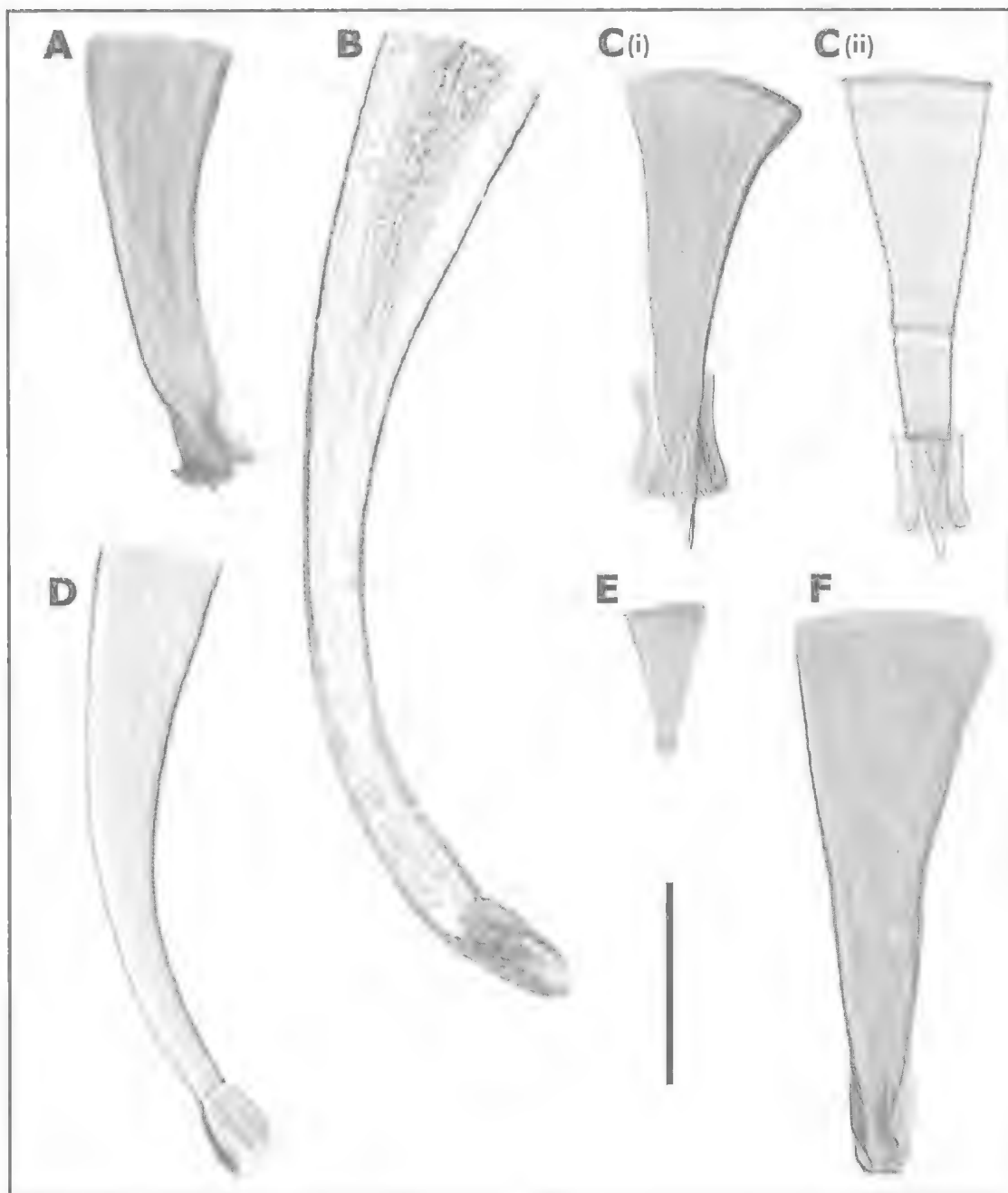


FIG. 5. Nomarski interference contrast photomicrographs of De Faure's preparations of the whole cirri of *Temnosewellia* species. A, *T. chaeropsis* QMG217457. B, *T. christineae* QMG217462. C, *T. dendyi* - (i) QMG217488 ex *Cherax depressus*, (ii) QMG217497 ex *C. robustus*. D, *T. minor* QMG217482. E, *T. phantasmella* QMG217475. F, *T. punctatus* QMG217469. Scale = 100µm.

Dam near Byford (32°13'S 116°00'E), 22/Feb/1990, L. Evans, Form/Hx; QMGL18837-18838 (LS[3,2]), Form/H&E; QMGL18839-18840 (WM) WA Fisheries, Fish Health Dept., 6/Aug/1991, T. Thorne, Form/Hx;

QMGL18841-18844 (LS[2,2,2,1]), Form/H&E; QMGL18845 (WM) Western Australia, Nov/1989, L. Evans, Form/Hx; QMGL18846-18847 (LS[1,1]), Form/H&E; QMGL18848-53 (WM) Margaret R. Marron

fam. 10 km S Margaret R. (34°00.8'S 115°09.5'E). 23/Jan/1992, L.R.G. Cannon & K.B. Sewell, Form/Hx. SOUTH AFRICA: QMGL18868-18872 (WM) (in culture), 1991, A. Avenant-Oldewage, Form/Carmine; QMGL18873-18875 (WM) (in culture), 1982, D.J. Kok, Form Carmine.

DESCRIPTION. *General Anatomy.* Medium sized temnocephalan with pigment dorsally very variable but usually with some open patches (Fig. 3C); it extends forward from the eyes mainly into the proximal or basal regions of the central 3 tentacles; ventral pigment only a tracery to about the level of the mouth. Although they can be overlooked, clusters of posterolateral glands occur (Cannon & Watson, 1996).

Reproductive System Female. Vesicula resorbens opens to a muscular chamber and then to the relative short muscular vagina with a powerful sphincter distally before opening to the common atrium. No evident seminal receptacles.

Male. Testes deeply notched on lateral borders, not generally overlapping. Cirrus gently curved with introvert only slightly inflated. Selected measurements are: QMG217478: S(93 × 67), I(25 × 19); QMG217479: S(98 × 58), I(33 × 19); QMG217480: S(72 × 52), I(34 × 22); QMG217481: S(305 × 89), I(34 × 18); QMG217482: S(294 × 61), I(37 × 18); QMG217483: S(343 × 70), I(41 × 15); QMG217484: S(58 × 21), I(40 × 19).

HOSTS. *Cherax destructor*, *C. dispar*, *C. depressus* and, in culture, *C. albidus*, *C. quadricarinatus* and *C. tenuimanus* (Parastacidae).

LOCALITY. Found in the whole of the Murray-Darling system Qld, NSW, Vic and SA, and also coastal Queensland from Marlborough south where *Cherax depressus* and *C. dispar* occur. Found on cultured and free range marron, *C. tenuimanus*, in WA and elsewhere where this crayfish is cultured, notably Japan (Oki, Tamura, Takai & Kawakatsu, 1995) and South Africa. This worm has been found also on European crayfish presumably contaminated in aquaria holding Australian crayfish (Xylander, 1997), but now is believed to have escaped into streams in Bavaria, Germany (Xylander, pers. comm.).

REMARKS. Haswell (1888, 1893) clearly characterised this species. No types exist, but there seems little possibility now of confusion about the identity of this worm which is so common and widespread. The most striking difference or discrepancy with the original accounts (Haswell, 1888, 1893) is the presence of

postero-lateral glands (Cannon & Watson, 1996). These glands do not stain consistently and can easily be overlooked. *T. minor* is now known to be the worm infecting cultured marron in South Africa. It appears to have a catholic choice of hosts and obviously may become widespread.

Reports of this species from *Cherax punctatus* by Cannon & Jennings (1987) should be referred to *C. depressus*.

Details of the cirrus are essentially as presented by Haswell (1893) as can be seen from the de Faure's preparation (Fig. 5D; 6D). We observed no more than minor differences in proportions in specimens from different localities. Furthermore, our specimens mostly resemble Haswell's (1893, pl. 15, fig. 1) regarding the distribution of the testes i.e. they are clearly separated and not overlapping as his text states (though with equivocation). The pattern of the mosaic of *T. minor* ex *Cherax destructor* from the Condamine R., Warwick was described and figured by Joffé & Cannon (1998: figs 2C,F-G, 3C).

***Temnosewellia punctata* sp. nov.**
(Figs 3D, F, G, 5F, 6F)

ETYMOLOGY. In reference to the punctate coalescence of the dorsal pigment.

MATERIAL. HOLOTYPE: QMGL18857 (WM), ex *Cherax* cf. *quinquecarinatus*, Carburup R., 2 km N of Carburup at railway bridge, WA (33°40.8'S 115°11.8'E) 23/Jan/1992, L.R.G. Cannon & K.B. Sewell, HW/Form/Hx. PARATYPES: QMGL18858-18859 (WM); QMGL18860-18861 (LS[1,3]), HW/Form/H&I.

OTHER MATERIAL. Ex *Cherax* cf. *quinquecarinatus*. WA: QMGL18862-18863 (WM), Carburup R., 2 km N of Carburup at railway bridge (33°40.8'S 115°11.8'E) 23/Jan/1992, L.R.G. Cannon & K.B. Sewell, HW/Form/Hx; QMGL18864 (LS[2]), HW/Form/H&I; QMG217468-217469 (CP) HW/70% Ale/deF; QMG217497 (CP); QMG217470-217471 (PP); QMG217498 (PP).

Ex *Cherax tenuimanus*. WA: QMGL18865-18867 (WM), at catchment weir, Margaret R. (33°57.0'S 115°05.2'E), 23/Jan/1992, L.R.G. Cannon & K.B. Sewell, HW/Form/Hx.

DESCRIPTION. *General Anatomy.* Medium sized temnocephalan with distinctive pattern of pigment with punctiform clusters (Fig. 3D). Posterior gland reservoirs numerous and spread in a wide arc along the posterior margin of the body. Selected measurements are: QMGL18857 (H): B(1432 × 858), LE(1314), SD(414), PD(166); PH(225 × 260), EA(142 × 77 & 178 × 77), ED(41 & 47); AI(189 × 130 & 237 × 124), PI(237 × 118 & 245 × 160); QMGL18858 (P): B(1686 × 746),

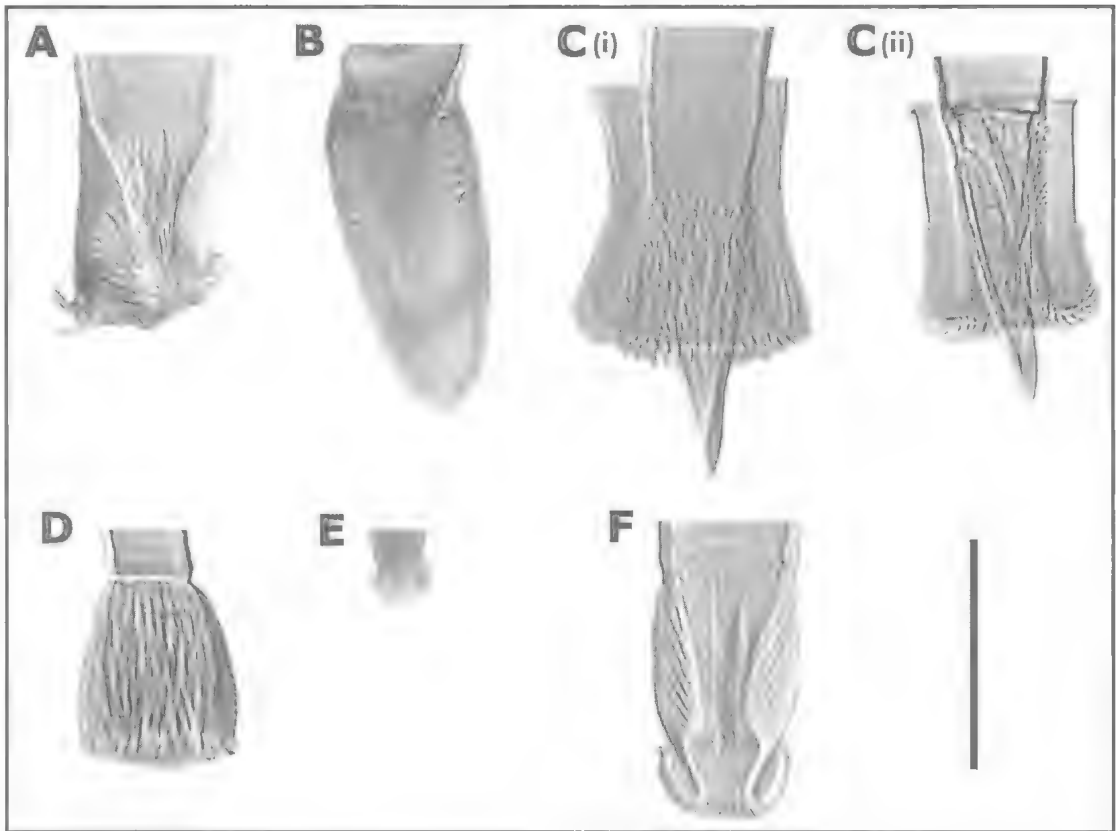


FIG. 6. Nomarski interference contrast photomicrographs of De Faure's preparations of the introverts of cirri of *Temnosewellia* species. A, *T. chaeropsis* QMG217457. B, *T. christineae* QMG217462. C, *T. dendyi* - (i) QMG217488 ex *Cherax depressus*, (ii) QMG217497 ex *C. robustus*. D, *T. minor* QMG217482. E, *T. phantasmella* QMG217475. F, *T. punctata* QMG217469. Scale = 50 μ m.

LE(1065), SD(367), PD(142); PH(294 \times 254), EA(89 \times 65 & 89 \times 65), ED(36 & 36); AT(124 \times 112 & 154 \times 101), PT(219 \times 130 & 195 \times 130); QMGL18859 (P): B(1941 \times 805), LE(1219), SD(385), PD(148); PH(195 \times 278), EA(101 \times 71 & 95 \times 77), ED(47 & 47); AT(189 \times 118 & 183 \times 118), PT(231 \times 130 & 219 \times 136).

Reproductive System. Female. Vesicula resorbens with 4 small seminal receptacles at its base; ovary joins below these at the top of a long, narrow, proximal vagina which enters an extremely voluminous and highly muscular distal vagina. This in turn opens via a strong distal sphincter to a small common atrium.

Male. A moderately small ejaculatory sac joins the top of the cirrus bulb with the prostate glands and the ejaculatory duct. Cirrus gently curved with slightly inflated introvert (Fig. 6F). Selected measurements are: QMG217468: S(222 \times 93),

I(72 \times 31); QMG217469: S(223 \times 100), I(70 \times 30); QMG217497: S(164 \times 62), I(75 \times 30).

HOSTS. *Cherax* cf. *quinquecarinatus* and *C. tenuimanus* (Parastacidae)

LOCALITY. Southwestern WA.

REMARKS. This species most closely resembles *T. chaeropsis* with which it shares not only the posterior gland reservoirs, but also the large and muscular distal vagina which clearly must serve as an ootype or uterus. The most striking differences are the pigment pattern which in this species is distinctively punctate, not a tracery, and the much smaller, but more numerous and more broadly distributed posterior gland reservoirs.

***Temnosewellia phantasmella* sp. nov.**
(Figs 3E, 5E, 6E)

ETYMOLOGY. Latin, from *phantasma* = a spirit: literally a little spirit from the appearance of the pigment pattern.

MATERIAL. HOLOTYPE: QMGL18893 (WM), ex *Cherax rhynchotus*, Lake Wicheura, Cape York, Qld (10°46'S 142°34'E) 27/Sep/1990, P.J.F. Davie & J.W.Short, 70% Alc/Hx. PARATYPES: QMGL18894-18895 (WM); QMGL18891-18892 (LS[1,2]), Alc/H&E.

OTHER MATERIAL. Ex *Cherax rhynchotus*. QLD: QMGL18889 (WM), Lake Wicheura, Cape York, (10°46'S 142°34'E) 27/Sep/1990, P.J.F. Davie & J.W.Short, Alc/Hx; QMGL18896 (WM); G217472-217475 (CP) Alc/deF; QMG217476-217477 (PP); QMGL18890 (LS[2]), Lake Boronto, near Somerset, Cape York (10°45'S 142°35'E) 25/Sep/1974, G.B. Monteith, Alc/H&E.

DESCRIPTION. *General Anatomy*. Small slender worm with eyes set very close together and a distinctive pigment pattern concentrated anteriorly leaving lacunae about excretory ampullae. Pharynx robust and sucker set well posterior; prominent postero-lateral glands. Selected measurements are: QMGL18893 (H): B(1609 × 337), LE(680), SD(148), PD(71); PH(130 × 124), EA(59 × 41 & 53 × 41), ED(24 & 24); AT(118 × 107 & 136 × 107), PT(142 × 77 & 136 × 89); QMGL18894 (P): B(840 × 320), LE(562), SD(148), PD(77); PH(83 × 77), EA(41 × 36 & 41 × 36), ED(18 × 18); AT(118 × 59 & 118 × 65), PT(83 × 59 & 83 × 65); QMGL18895 (P): B(746 × 266), LE(485), SD(130), PD(53); PH(107 × 59), EA(41 × 36 & 41 × 30), ED(18 & 18); AT(95 × 53 & 77 × 59), PT(65 × 53 & 71 × 65).

Reproductive System. Female. The vesicula resorbens opens to a short muscular vagina and then to a large common atrium with a low epithelium.

Male. Seminal vesicle large and ejaculatory sac a small bulb enter the base of the cirrus side by side; no evident copulatory bulb. Selected measurements are: QMG217472: S(79 × 45), I(16 × 12); QMG217473: S(72 × 34), I(15 × 11); QMG217474: S(64 × 29), I(16 × 11); G217475: S(76 × 43), I(17 × 12).

HOST. *Cherax rhynchotus* (Parastacidae)

LOCALITY. Known only from Cape York, Queensland.

REMARKS. This small worm is characterised by a cirrus dramatically smaller than in any other *Temnosewellia* from *Cherax*. Its closest relative appears to be *T. butlerae* known from the

freshwater crab, *Holthuisana transversa*, taken from Augathella, western Queensland. However, the pigment pattern is dissimilar: in *T. phantasmella* there is an anterior concentration spreading laterally and surrounding the excretory ampullae as two clear lacunae, but in *T. butlerae* there is a small concentration before the eyes and then a straggling tracery in about 3 longitudinal bands. The eyes in *T. butlerae* are set farther apart, the common atrium has very well developed epithelium and the seminal vesicle and ejaculatory sac are slender. Furthermore, the hosts and localities are very different.

***Temnosewellia* sp.**

MATERIAL. Ex *Cherax punctatus*. QLD: QMGL18886 (WM), Dingo Ck near Traveston (26°19'S 152°47'E) Mar/1973, S.R. Monteith, Alc/Hx; QMGL18887 (LS[2]), Alc/H&E.

DESCRIPTION. A small and apparently eyeless species.

REMARKS. The single specimen QMGL18886 cannot be readily referred to another species. The host crayfish is a deep burrowing one and may therefore rarely emerge. An eyeless species of worm from a host that rarely emerges into daylight is thus not unexpected. Haswell (1893) reported the eyes to be 'very small' in *T. engaei* (Haswell, 1893) from the burrowing land crayfish *Engaeus fossor* from Gippsland. Similarly, the temnocephalans reported from the burrowing isopod *Phreatoicopsis terricola*, *T. caeca* (Haswell, 1900) and *T. geonoma* (Williams, 1980), are blind and without pigment.

Teratological specimens of temnocephalans without eyes, however, are sometimes encountered, but usually can be readily placed. It is not possible to describe this species formally as there is far too little material and we are reluctant to infer too much about the absence of eyes in one specimen.

DISCUSSION

Cannon & Sewell (1995) showed that subtle differences in male copulatory structures can indicate species separation in temnocephalans (*Craspedella spenceri* and *C. simulator*); such differences are not readily apparent within *Temnosewellia*, e.g. *T. minor*. We recognise, however, that only a thorough meristic study from live preparations using de Faure's fluid would reveal such differences. Furthermore, life history and ecology of *Temnosewellia* spp. suggests no more than regional variations will be

found: these worms are active external dwelling worms which colonise new hosts much more readily than do species of *Craspedella* which are found in the sheltered branchial cavity and consequently show higher host specificity. Clearly the two WA species of *Temnosewellia* are close as would be expected. Low host specificity is particularly manifest, however, with *T. minor* which has the potential to spread around the world.

The worms *T. acirra* and *T. dendyi* which occur predominantly in the sheltered branchial habitat of *Cherax destructor* may be shown to exhibit niche separation or competition. This matter needs investigation, for the two species were confused from live study: only a microscopic examination of the male copulatory structures can distinguish them.

Questions arise concerning the recent biogeography of *T. minor* from *C. dispar* and *C. depressus*. *T. minor* is widespread in the Murray Darling system and has been translocated around the country and the globe in aquaculture. Its occurrence on the two small *Cherax* from coastal Queensland seems to indicate a recent intermingling of streams across the watershed of the Great Dividing Range. Musyl & Keenan (1992) suggested this as an explanation for some freshwater fish in central Queensland being found on both sides of the divide, i.e. from both the western Warrego and coastal Dawson drainages. *T. minor* could have spread south from here along the coast to include both *C. dispar* and *C. depressus* as hosts: molecular techniques may be able to indicate when this may have happened. On the coast, *T. christineae* appears the ecological homologue to *T. minor*. Is competition between these species evident?

Other Australian species currently in *Temnocephala* s. l. and found, for example, on crabs, shrimps and crayfish have also been tentatively assigned to *Temnosewellia* by Damborenea & Cannon (2001), pending more thorough review. Further, the eyeless worm specimen from *C. punctatus*, a rarely encountered burrowing crayfish with a limited distribution, is likely to prove a new species (other eyeless species are known), but more specimens are needed to rule out any teratology.

The exclusion of *T. rouxi* from this account is tentative. Though previously known only from Aru Is. (Indonesia), Cannon (1991) reported it from cultured red-claw (*Cherax quadricarinatus*) from the NT. It and *Temnocephala*

semperi Weber, 1889 from Asian freshwater crabs may belong to a separate, as yet undescribed, genus (B.I. Joffe, pers. comm.).

ACKNOWLEDGEMENTS

We would like to acknowledge the support of ABRS who funded the initial studies and to the Queensland Museum. Mrs Zeinab Khalil assisted ably and cheerfully with laboratory routines.

LITERATURE CITED

- AVENANT-OLDEWAGE, A. 1993. Occurrence of *Temnocephala chaeropsis* on *Cherax tenuimanus* imported into South Africa, and notes on its infestation of an indigenous crab. South African Journal of Science 89: 427-428.
- CANNON, L.R.G. 1986. Turbellaria of the World - a guide to Families and Genera. (Queensland Museum: Brisbane).
1991. Temnocephalan symbiotes of the freshwater crayfish *Cherax quadricarinatus* from northern Australia. Hydrobiologia 227: 341-347.
1993. New temnocephalans (Platyhelminthes): ectosymbionts of freshwater crabs and shrimps. Memoirs of the Queensland Museum 33: 17-40.
- CANNON, L.R.G. & JENNINGS, J.B. 1987. Occurrence and nutritional relationships of four ectosymbiotes of the freshwater crayfishes *Cherax dispar* Riek and *Cherax punctatus* Clark (Crustacea: Decapoda) in Queensland. Australian Journal of Marine and Freshwater Research 38: 419-427.
- CANNON, L.R.G. & JOFFE, B.I. 2001. The Temnocephalida. Pp.83-91. In Littlewood, D.T.J. & Bray, R.A. (eds) Interrelationships of the Platyhelminthes. (Taylor & Francis: London).
- CANNON, L.R.G. & SEWELL, K.B. 1994. Symbionts and biodiversity. Memoirs of the Queensland Museum 36: 33-40.
1995. Craspedellinae subfamily nov. (Platyhelminthes: Temnocephalida) from the branchial chamber of Australian crayfish. Memoirs of the Queensland Museum 38: 397-418.
2001. Observations on *Dactylocephala madagascariensis* (Vayssière, 1892) a temnocephalan with twelve tentacles from Madagascar. Zoosystema 23: 11-17.
- CANNON, L.R.G. & WATSON, N. 1996. On the posterior rhabdoid glands of *Temnocephala minor*. Australian Journal of Zoology 44: 69-73.
- DAMBORENEA, C. & CANNON, L.R.G. 2001. On neotropical *Temnocephala* (Platyhelminthes). Journal of Natural History (in press).
- HASWELL, W.A. 1888. On Temnocephala, an aberrant Monogenetic trematode. Quarterly Journal of Microscopical Science 28: 279-303.
1893. A Monograph on the Temnocephalae. Macleay Memorial Volume (Linnean Society of New South Wales): 94-152.

- HETT, M.L. 1925. On a new species of *Temnocephala* (*T. chaeropsis*) (Trematoda) from West Australia. Proceedings of the Zoological Society of London: 569-575.
- JOFFE, B.I. & CANNON, L.R.G. 1998. The organisation and evolution of the mosaic of the epidermal syncytia in the Temnocephalida, (Plathelminthes: Neodermata). Zoologischer Anzeiger 237: 1-14.
- MERTON, H. 1913. Beiträge zur Anatomie und Histologie von *Temnocephala*. Abhandlungen Senckenbergische Naturforschende Gesellschaft 35: 1-58.
- MITCHELL, S.A. & KOK, D.J. 1988. Alien symbionts introduced with marron from Australia may pose a threat to aquaculture. South African Journal of Science 84: 877-878.
- MUSYL, M.K. & KEENAN, C.P. 1992. Population genetics and zoogeography of Australian freshwater Golden Perch, *Macquaria ambigua* (Richardson 1845) (Teleostei: Percichthyidae), and electrophoretic identification of a new species from the Lake Eyre Basin. Australian Journal of Marine and Freshwater Research 43: 1585-601.
- OKI, I., TAMURA, S., TAKAI, M. & KAWAKATSU, M. 1995. Chromosomes of *Temnocephala minor*, an ectosymbiotic turbellarian on Australian crayfish found in Kagoshima Prefecture, with karyological notes on exotic turbellarians found in Japan. Hydrobiologia 305: 71-77.
- SEWELL, K.B. & CANNON, L.R.G. 1996. The taxonomic status of *Didymorchis paranephropis* Haswell, 1900. Memoirs of the Queensland Museum 42(2): 585-595.
1998. New temnocephalans from the branchial chamber of Australian *Euastacus* and *Cherax* crayfish hosts. Proceedings of the Linnean Society of New South Wales 119: 21-36.
- XYLANDER, W.E.R. 1997. Epidermis and sensory receptors of *Temnocephala minor* (Plathelminthes, Rhabdocoela, Temnocephalida): an electron microscopic study. Zoomorphology 117: 147-154.

RANGE EXTENSIONS FOR TWO POORLY KNOWN QUEENSLAND SNAKES. *Memoirs of the Queensland Museum* 46(2): 400–2001 – *Furina dunmali* (Worrell, 1956) and *Suta dryeri* (Worrell, 1956) are amongst the least known of Australia's many poorly known elapids. The former, narrowly confined to mid and southeastern Queensland, is known from only 2 specimens in the Australian Museum and is a 'vulnerable' species (Longmore, 1986; Ingram & Raven, 1991; McDonald et al., 1991; Cogger et al., 1993; IUCN Council, 1994; Nature Conservation Legislation Amendment Regulation (No. 2) 1997). *Suta dryeri* occurs from southern Queensland to northern Victoria and, if museum collections are any guide, is more common. It has no special conservation status (Longmore, 1986; Ingram & Raven, 1991) but its taxonomic status is uncertain (Cogger, 2000; Cogger et al., 1993).

During recent surveys in Queensland's Brigalow Belt and Desert Uplands Bioregions, one specimen of each species was discovered and both extend the known distributions.

Furina dunmali

This snake, collected from the outskirts of Clermont (22°45'S, 147°35'E), in the Northern Brigalow Belt Bioregion, was presented to the Emerald office of the Queensland Parks and Wildlife Service for identification (late summer, 1999). The specimen was identified as *F. dunmali* and lodged with the Queensland Museum (QM173000). It was melanistic, lacking pale diffuse blotches-barring on the upper lips. (Such barring occurs on all specimens in the QM collection, P. Couper, pers. comm.) Vegetation communities adjacent to Clermont include *Eucalyptus coolabah* (coolibah) and *L. populnea* (poplar box) woodlands on alluvials and *F. crebra* (narrow-leaved ironbark) and *Acacia rhodoxylon* (rosewood) on shallow rocky soils.

Two specimens in the Australian Museum came from the southern Brigalow Belt (27°13'S, 149°41'E) and the South-east Queensland Bioregion (27°37'S, 151°37'E). The Queensland Museum has 7 specimens from the southern Brigalow Belt (Oakey 27°26'S, 151°43'E; Miles 26°4'S, 150°14'E; Taroom 25°18'S, 149°1'E; and Maidenwell 26°51'S, 151°48'E); two from the South-east Queensland Bioregion (Archookoorra 26°44'S, 151°48'E; and Gladstone 23°51'S, 151°16'E); and one from the Northern Brigalow Belt (Mt Archer, via Rockhampton 23°21'S, 150°34'E).

The Clermont specimen of *F. dunmali* extends the distribution approximately 300km to the north west of Mt Archer. It is the first from the Central Highlands of the northern Brigalow Belt Bioregion, an area assailed by fire (C. Arnold).

Suta dryeri

An adult *Suta dryeri* (nomenclature after Hutchinson, 1990) was removed by the authors from a pitfall trap on the 12/11/99, while surveying in poplar box open woodland on Monklands Station via Alpha, Southern Desert Uplands Bioregion (23°28'48"S, 146°25'13"E). Identification was verified by P.J. Couper of the Queensland Museum and the specimen lodged in the Queensland Museum collection (QM172321). The locality was a large (about 40,000ha) poplar box and silver-leaved ironbark woodland with an open grassland understorey dominated by *Tristida* spp. (wiregrasses), *Bothriochloa ewartiana* (desert bluegrass), *Chrysopogon fallax* (golden beardgrass), *Heteropogon contortus* (black spear grass), and *Trindlia mitchellii* (buck spinifex) on texture contrast soils.

Suta dryeri (Worrell, 1956) has an unstable taxonomic history. It has been placed in *Denisia*, *Unecyris*, *Rhinoplocephalus* and *Suta*; and has been treated as a subspecies of *Suta spectabilis* (Krell, 1869), e.g. Worrell,

1956; Longmore, 1986; Wilson & Knowles, 1988; Hutchinson, 1990; Ingram & Raven, 1991; Ehmann, 1992; Cogger, 2000. The species is poorly known and its distribution ill-defined. Covacevich & Couper (in Ingram & Raven, 1991) showed it to be confined primarily (in Queensland) to the eastern Mulga Lands, Southern Brigalow Belt, and South-east Queensland Bioregions. Two specimens have also been collected from the northern Brigalow Belt, Newlands Mine near Mackay (21°11'S, 147°54'E; QMJ65065), and Townsville (19°16'S, 146°49'E; AMR119422).

The Monklands specimen is the first record from Queensland's Desert Uplands Bioregion. The nearest *S. dryeri* locality is at Mt Moffatt in the Carnarvon Ranges (20°35'S, 140°13'E; QMJ59373), 225km to the southeast; the Newlands Mine record is 300km to the northeast. *Suta dryeri* is now known to range through the Mulga Lands, Southeast Queensland, Brigalow Belt and the Desert Uplands Bioregions.

Acknowledgments

We thank the Natural Heritage Trust for funding support and the Queensland Parks and Wildlife Service, Queensland Museum, Queensland Herbarium, Griffith University, Tropical Savannas Cooperative Research Centre and the Parks and Wildlife Commission of the Northern Territory for in-kind support for the survey component of this work. Jeanette Covacevich, Patrick Couper and Andrew Arney of the Queensland Museum and Ross Sadlier of the Australian Museum kindly assisted with the preparation of this note. Thanks also to Juliana McCosker and Richard Johnson who offered comments on an earlier draft.

Literature Cited

- COUGER, H.G. 2000. Reptiles and amphibians of Australia, 6th Edition. (Reed New Holland: Sydney).
- COUGER, H.G., CAMERON, J.E., SADI, J.R. & EGGLE, P. 1993. The action plan for Australian reptiles. (Australian Nature Conservation Agency, Canberra).
- EHMANN, H. 1992. Encyclopedia of Australian animals - Reptiles (Angus & Robertson: Pymble, NSW), pp. 495.
- HUTCHINSON, M. 1990. The generic classification of the Australian terrestrial elapid snakes. *Memoirs of the Queensland Museum* 29(2): 397–405.
- INGRAM, G.J. & RAVEN, R.J. (eds) 1991. An atlas of Queensland's frogs, reptiles, birds and mammals. (Queensland Museum, Brisbane).
- IUCN COUNCIL 1994. IUCN Red List Categories. Prepared by the IUCN Species Survival Commission as approved by the 40th meeting of the IUCN Council, Gland, Switzerland, 30 Nov., 1994. (IUCN Council: Gland).
- LONGMORE, R. 1986. Atlas of elapid snakes of Australia. Australia Flora and Fauna Series 7. (Australian Government Publishing Service: Canberra).
- MCDONALD, D., K.R., COVACEVICH, J.A., INGRAM, G.J. & COUPER, P.J. 1991. The status of frogs and reptiles. Pp. 328–345. In Ingram, G.J. & Raven, R.J. (eds), An atlas of Queensland's frogs, reptiles, birds and mammals. (Queensland Museum: Brisbane).
- WILSON, S.K. & KNOWLES, D.G. 1988. Australia's reptiles: A photographic reference to the terrestrial reptiles of Australia. (Collins: Sydney).
- WORRELL, L. 1956. A new snake from Queensland. *Australian Zoologist* 12: 202–205.

David Hannah and Nicole Y. Thurgate. Queensland Parks and Wildlife Service, PO Box 906, Emerald 4720, Australia. 3 November 2000.

ADDITIONS TO THE ROSTROCONCH FAUNA OF AUSTRALIA AND CHINA

ALEX G. COOK AND NATALIE CAMILLERI

Cook, A.G. & Camilleri, N. 2001 06 30: Additions to the rostroconch fauna of Australia and China. *Memoirs of the Queensland Museum* 46(2): 401-407. Brisbane. ISSN 0079-8835.

Eight taxa of rostroconch are described from stratigraphically and geographically dispersed localities in Australia; *Euchasma caseyi* and *Euchasma colliveri* sp. nov. from the Ordovician (Caradoc) of Tasmania; *Kandosoconcha pambertoni* gen. et sp. nov. from the Lochkovian-Pragian Yellowmans Creek Beds near Kandos, NSW; and *Hippocardia* sp. from the Lochkovian-Pragian Martins Well Limestone, NQ. *Conocardium sowerbyi* de Koninck, is described from the Emsian Brogans Creek Lst of the Capertee Valley, and a neotype for the species is designated. A single rostroconch is described from the Middle Devonian of Guangxi, China. Rostroconchs are described for the first time from the Carboniferous of Australia. □ *Rostroconchs, new taxa, Ordovician, Devonian, Carboniferous, Australia, China.*

Alex G. Cook & Natalie Camilleri Queensland Museum PO Box 3300, South Brisbane 4101, Australia (e-mail: alexc@qm.qld.gov.au); 20 November 2000.

Ordovician rostroconchs are known from central Australia (Pojeta, et al., 1977) and Tasmania (Etheridge, 1883; Pojeta, 1979). *Euchasma caseyi* Pojeta et al., 1977 and *E. colliveri* sp. nov. are described from the Gordon Group near Zeehan Tasmania, in shales from near the Zeehan Smelters Quarry which Banks & Burrett (1989) correlated with their OT17 or OT18 faunal assemblage (Caradoc).

Known Australian Devonian rostroconchs come mainly from the Lower Devonian of SE Australia (de Koninck, 1876; Creswell, 1893; Etheridge, 1881; Chapman, 1908; Fletcher, 1943; Talent, 1956; Talent & Philip, 1956; Tassell, 1982) with only *C. gogoense* Fletcher (1943), known from Upper Devonian of the Canning Basin WA.

Early Devonian material described herein comes from: 1) Yellowmans Creek Beds, near Kandos NSW; 2) Brogans Creek Lst in the upper Capertee Valley NSW, and 3) the Martins Well Limestone Member of the Shield Creek Fm, Broken River Province, north Queensland.

The Yellowmans Creek Beds are a thick sequence of shales with minor limestone and calcareous shales near the base (Pemberton et al 1994, Colquhoun 1996). *Kandosoconcha pambertoni* gen. et sp. nov. is derived from the lowermost 10m of the formation above the Kandos #1 limestone quarries. The locality has yielded *Ozarkadina remschiedensis remschiedensis*, *Amydrotaxis sexidentata* (Mawson in Cook, 1988) and is regarded as late Lochkovian to earliest Pragian.

The Brogans Creek Limestone has been regarded as lateral equivalent of the Carwell Creek Group (Pemberton et al, 1994). Colquhoun (1995) suggested an early Emsian age for the limestone based on conodonts. Shelly faunas currently under investigation show strong species-level similarity with the 'Receptaculites' Limestone of Taemas, and thus for the single horizon containing *Conocardium sowerbyi* de Koninck, a late Emsian age is probable.

The Martins Well Limestone Member of the Shield Creek Formation is regarded as spanning the Lochkovian-Pragian boundary (Jell et al., 1993). *Hippocardia* sp. were collected in the uppermost part and are here regarded as Pragian.

Conocardium gogoense Fletcher 1943 has been recovered from a silicified fauna in the Pillara Limestone (Frasnian) in the Hull Range, Canning Basin WA. (cf. Playford & Lowry, 1966). A paucity of biostratigraphically-useful fossils from the Pillara Limestone in the Hull Range make exact placement of the occurrence within the Frasnian impossible at present.

Fletcher (1943) concluded there was only one vague reference to Australian Carboniferous rostroconchs. The specimens described herein are from the Utting Calcarenite, Utting Gap identified by Roberts (1971) as Viséan in age.

Terminology follows Pojeta & Runnegar (1976) and Pojeta (in Boardmann et al., 1987).

SYSTEMATIC PALAEONTOLOGY

Phylum MOLLUSCA

Class ROSTROCONCHIA Pojeta, Runnegar,
Morris & Newell, 1972

Order CONOCARDIOIDA Neumayr, 1891

Superfamily EOPTERIOIDEA Miller, 1889

Family EOPTERIIDAE Miller, 1889

Euchasma Billings, 1865***Euchasma caseyi*** Pojeta, Gilbert-Tomlinson &
Shergold, 1976
(Fig. 1A-E)*Euchasma caseyi* Pojeta, Gilbert-Tomlinson & Shergold
1976: 27, pl. 20, figs 8-15, pl. 21, figs 1-9, pl. 23, figs
1-10, pl. 24, figs 1-5.MATERIAL. QMF37321-37323, two conjoined valves
and a fragmentary right valve, from QML901, Zeehan
Smelters Quarry, Zeehan Tasmania.DESCRIPTION. Shell medium sized, up to 10.8
mm long, 11.4mm high, 8.2mm wide; laterally
expanded, posterior outline circular, oblique
straight anterior face, very weakly concave.
Rostrum prominent, extending at least two thirds
along the dorsal margin. Anterior faces reclined
60° from horizontal, with modest ribs stronger
towards the gape. Gape a characteristic 'key hole'
shape, oval with invagination above and slit like
with interlocking denticles below. Posterior shell
dominated by evenly spaced ribs.REMARKS. The only slight difference between
this and the Georgina Basin material Pojeta et al.
(1976) is its coarser denticulation in the anterior
gape. This species differs from *E. colliveri* by the
architecture of the gape, weaker ribs and lack of
the prominent carina.***Euchasma colliveri*** sp. nov.
(Fig 1F-H)

ETYMOLOGY. For F.S.Colliver.

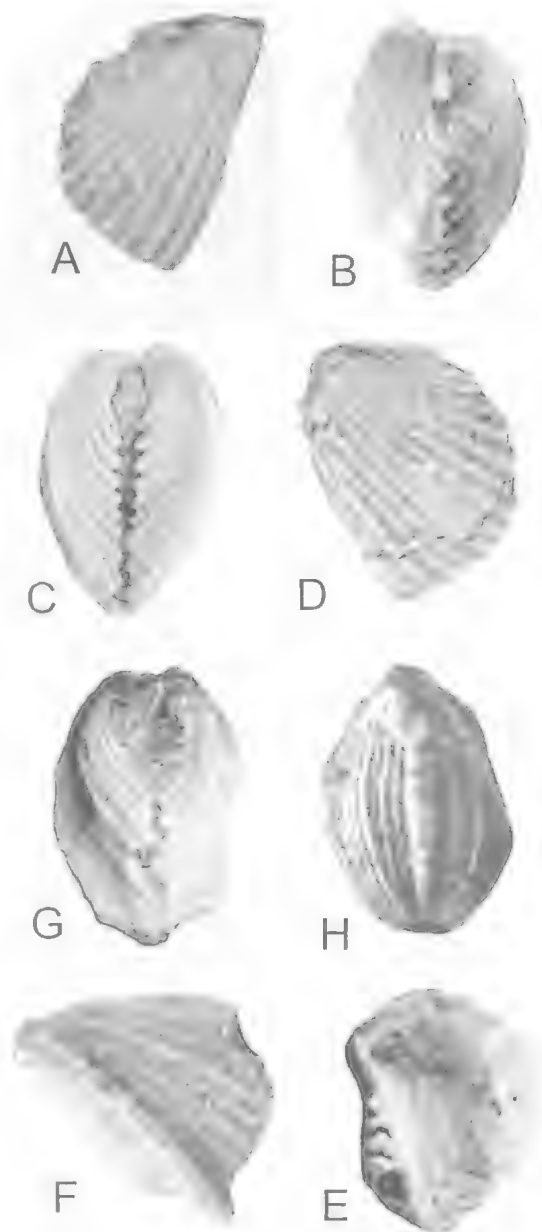
MATERIAL. Holotype: QMF37324 from QML901,
Zeehan Smelters Quarry, Zeehan Tasmania.DIAGNOSIS. Concave upper anterior face
convex lower anterior face, strong carina and
subtriangular outline.DESCRIPTION. Shell medium sized, oblique,
sub-triangular in outline, moderately inflated,
11.6mm long, 9.8mm high, 8.4mm wide.
Rostrum elongate, extending nearly to posterior
margin. Dorsal margin slightly arcuate. Anterior
face reclined at approximately 60° from the
horizontal, bordered from posterior shell by

FIG. 1. A-E, *Euchasma caseyi* Pojeta, Gilbert-Tomlinson & Shergold, 1976. A-C, QMF37322, right lateral, anteroventral and posterior views, $\times 2.4$. D, QMF37323, left lateral view, $\times 2.4$. E, QMF37324, internal view, $\times 2.4$. F-H, *Euchasma colliveri* sp. nov. Holotype QMF37321 $\times 2.4$, right lateral, posterior and dorsal views.

prominent raised carina. Anterior face concave near the dorsum, lacking ornament dorsally, convex towards the venter where it is adorned by strong but thin ribs and finer comarginal growth

lines. Posterior shell bears 6 ribs of subequal strength and numerous fine lines continuing the rib-dominant reticulation on the shell anterior to the main carina. Rostral clefts obscured.

REMARKS. Reticulation and the carina suggest affinities with *E. skvarkoi* Pojeta et al., 1976, but that taxon bears finer more numerous ribs, more robust ribs on the anterior face, and a less pronounced carina. The specimen differs from the type *E. blumenbachii* (Billings) (Pojeta & Runnegar, 1976, pl. 27) by having coarser ornament and a prominent carina.

Superfamily CONOCARDIOIDEA Miller, 1889
Family HIPPOCARDIIDAE Pojeta &
Runnegar, 1976

Hippocardia Brown, 1843

TYPE SPECIES. *Cardium hibernicum* Sowerby 1815 from the lower Carboniferous of Ireland.

Hippocardia sp.
(Fig. 2)

MATERIAL. QMF33798-33801 from QML541, Martins Well Limestone Member of the Shield Creek Formation, Broken River Province, north Queensland.

DESCRIPTION. Medium to large, up to 25.2mm long, 13.4mm high and approximately as wide as high. Dorsal margin straight with umbo mid-shell projecting slightly above hinge line. Prominent short rostrum situated just below dorsal margin. Snout long with wide anterior gape. A strong ridge and a smaller ridge posterior to it form a weak hood separating the posterior and anterior parts of the shell. Posterior face at approximately 60° to vertical with a concavity to rostrum. Ornament reticulate, evenly so on anterior shell, ribs stronger on posterior.

REMARKS. This poorly preserved material is generically assigned on the basis of the elongate snout and weak hood.

? Family HIPPOCARDIIDAE Pojeta &
Runnegar, 1976

Kandosconcha gen. nov.

TYPE SPECIES. *Kandosconcha pembertoni* sp. nov.

ETYMOLOGY. For the Kandos district, NSW.

DIAGNOSIS. Minute, trapezoidal, with prominent mid-shell carinae and intercalated ridges.



FIG. 2. *Hippocardia* sp. A-C, QMF33798, $\times 2$, left lateral, ventral and dorsal views. D, E, QMF33800, $\times 2$, right and left lateral views. F, QMF33801, $\times 2.4$, right lateral view

REMARKS. Gross anatomy, prominent carinae and reticulation suggests affinities with *Mulceodens* Pojeta & Runnegar or *Bigulea* Pojeta & Runnegar. *Mulceodens* was established for taxa with a constriction in the ventral part of the snout, but the restriction is lacking in the Kandos species. *Bigulea* has 2 rostral hoods, and a slit-like aperture. The Kandos species is closest to and shares the reticulation and trapezoidal shape of *B. visheyensis* Pojeta & Runnegar from the Silurian of Gotland differing by intercalation of ridges, no development of hoods, rather having carina.

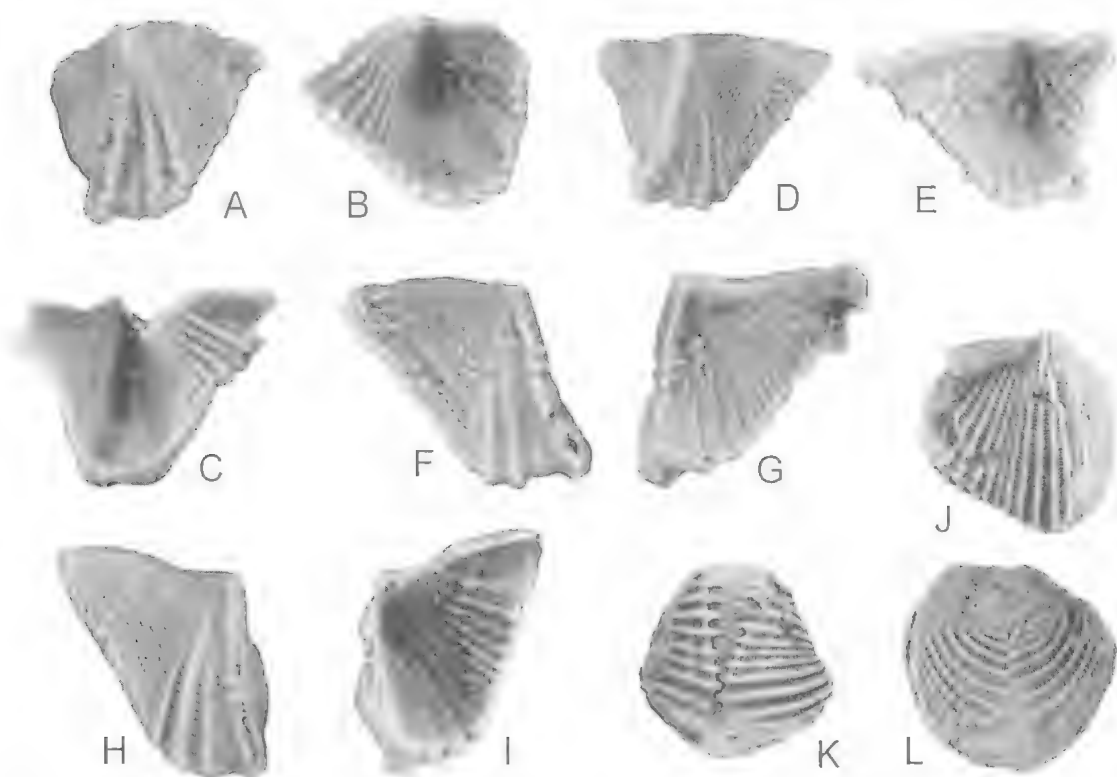


FIG. 3. A-I, *Kandoconcha pambertoni* gen. et sp. nov. A,B, Holotype QMF37325, $\times 20$. C, Paratype QMF37326, $\times 16$, left valve internal view. D, E, Paratype QMF37328, $\times 16$, right valve. F,G, Paratype QMF37327, $\times 10$, left valve. H,I, Paratype QMF37329, $\times 10$, left valve. J-L, *Conocardium* sp. 1. QMF41130, $\times 3.2$, left lateral, ventral and anterior views.

***Kandoconcha pambertoni* sp.nov.**
(Fig. 3A-I)

ETYMOLOGY. For John Pemberton.

MATERIAL. Holotype: QMF37325 (right valve), paratypes QMF37326-37330 from QML1026, top bench of Kandos #1 Quarry, W of Kandos NSW, Yellowmans Creek Beds, Early Devonian.

DIAGNOSIS. As for genus.

DESCRIPTION. Shell minute, up to 2.8mm long, 2.7mm high, trapezoidal, with 2 intermediate strength ribs between 2 major mid shell carinae. Dorsal margin nearly straight, umbones above dorsal margin. Anterior part of shell equantly triangular, with equally reticulate ornament, or on some specimens slightly dominant comarginal fine lines. Posterior portion smaller than anterior, with weak fine comarginal lines. Mid-shell with 3 or 4 strong ribs on the posterior ridge, the strongest forming a carina with next most robust ridge penultimate anterior also forming a carina. Minor ridges intercalated some

originating from mid shell, not from umbones. Reticulation continuing on mid-shell. Gape narrow with some denticulation. Rostrum unknown.

Family CONOCARDIIDAE Miller, 1889

***Conocardium* Bronn, 1835**

TYPE SPECIES. *Cardium elongatum* Sowerby 1815.

***Conocardium sowerbyi* de Koninck 1876**
(Fig. 4)

Conocardium sowerbyi de Koninck 1876:109; de Koninck 1898 (transl.): XX.

Conocardium sp. Tassell 1982: 2 pl. 1 fig.1.

TYPE. This taxon was not illustrated by de Koninck, 1876 and destruction of the material by fire rendered the name dubious in Tassell's (1982) opinion. Complicating this, the type locality was nebulously given by de Koninck as Yass district, with the host lithology as a black limestone. Thus the name is based on a non-existent type from an unclear locality. I here designate a neotype, ANU 36845 from the *Receptaculites* Limestone

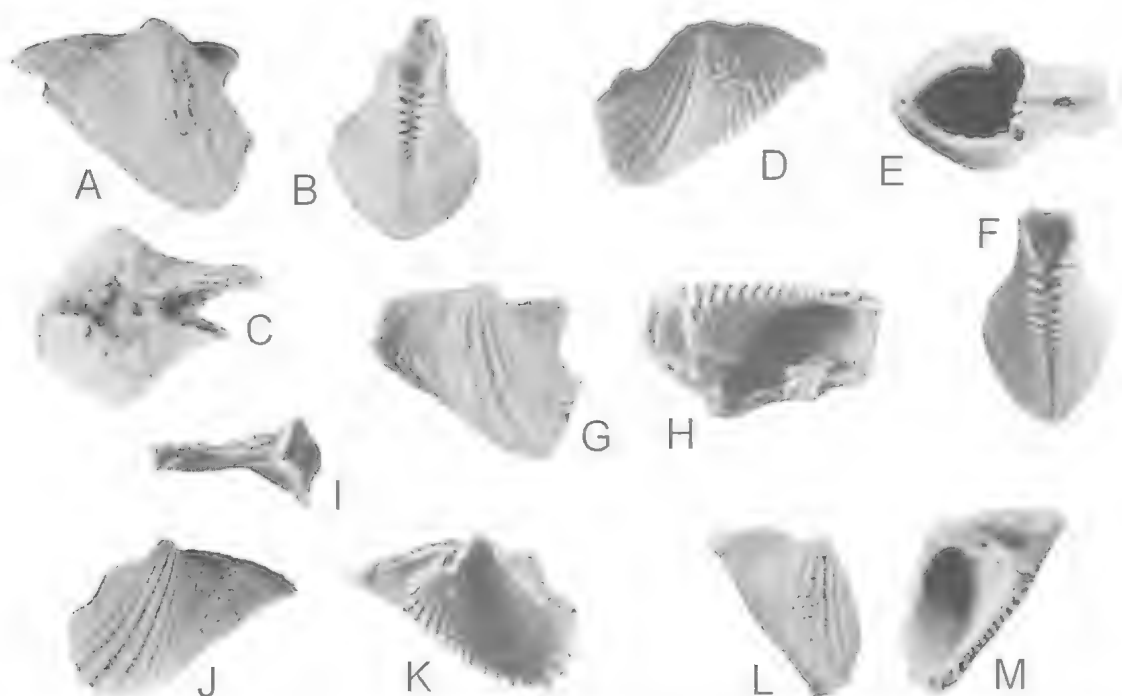


FIG. 4. *Conocardium sowerbyi* de Koninck, 1876. A-C, QMF37306, $\times 3.5$, left lateral, posterior and dorsal views. D-F, QMF37307, $\times 3.5$, right lateral, dorsal and anterior views. G,H, QMF37209, $\times 2.7$, left lateral and internal views. I, QMF37312, $\times 2.7$, dorsal view of snout. J,K, QMF37310, $\times 2.7$, right lateral and internal views. L,M, QMF37308, $\times 2.7$, left lateral and internal views.

described and figured as *Conocardium* sp. (Tassell, 1982). Given other taxa described by de Koninck, and Tassell (1982a), such as *Murchisonia turris* and *Mitchellia striatula*, are also abundant in the *Receptaculites* Limestone the most likely source of the conocardiid was this unit. Whilst the species was not illustrated by de Koninck and the name unused, there are reasonable grounds to conclude Tassell's material is topotypic and conspecific.

MATERIAL. QMF37306-QMF37312 from QML1027, Brogans Creek Limestone, Brogans Creek, Upper Capertee Valley, NSW. Devonian (Emsian).

DESCRIPTION. Small to medium sized, up to 11mm long, 8mm wide and 7mm high. Long rostrum just below and at slight angle to hinge. Umbo subcentral, well above hinge line. Valves moderately inflated. Anterior gape slit-like widening close to dorsum to form the oval snout, with elongate denticles. Short apertural shelves. Pegma at 45° to hinge. Broad flattened ribs on mid and posterior shell, widest and most pronounced on mid shell, ribs without intercalation. Anterior ribs finer. Fine growth lines present. Posterior-most shell and rostrum lacks ornament.

REMARKS. The narrow slit, broad ribs, and aperture confined to the end of the shell demonstrate that this material is conspecific with that described by Tassell (1982) and de Koninck's (1876).

***Conocardium gogoensis* Fletcher, 1943.**
(Fig. 5A,B)

MATERIAL. QMF36085, QMF42233 from QML1033, Pillara Limestone, Hull Range, Canning Basin, WA; Devonian (Frasnian).

DESCRIPTION. Moderately inflated, up 7mm long, and 6.5mm high, umbones well above dorsal margin. Antero-dorsum straight, rostrum not preserved. Posterior face at 30° from horizontal. Anterior surface with wide numerous flattened ribs. Posterior at least partially ornamented by finer ribs. Fine detail lacking due to coarse silicification.

REMARKS. Of the many hundreds of kilograms of limestone dissolved only these two specimens of rostroconch were recovered. Fletcher's (1943) specimens are similarly coarse ribbed, and equally long as high.

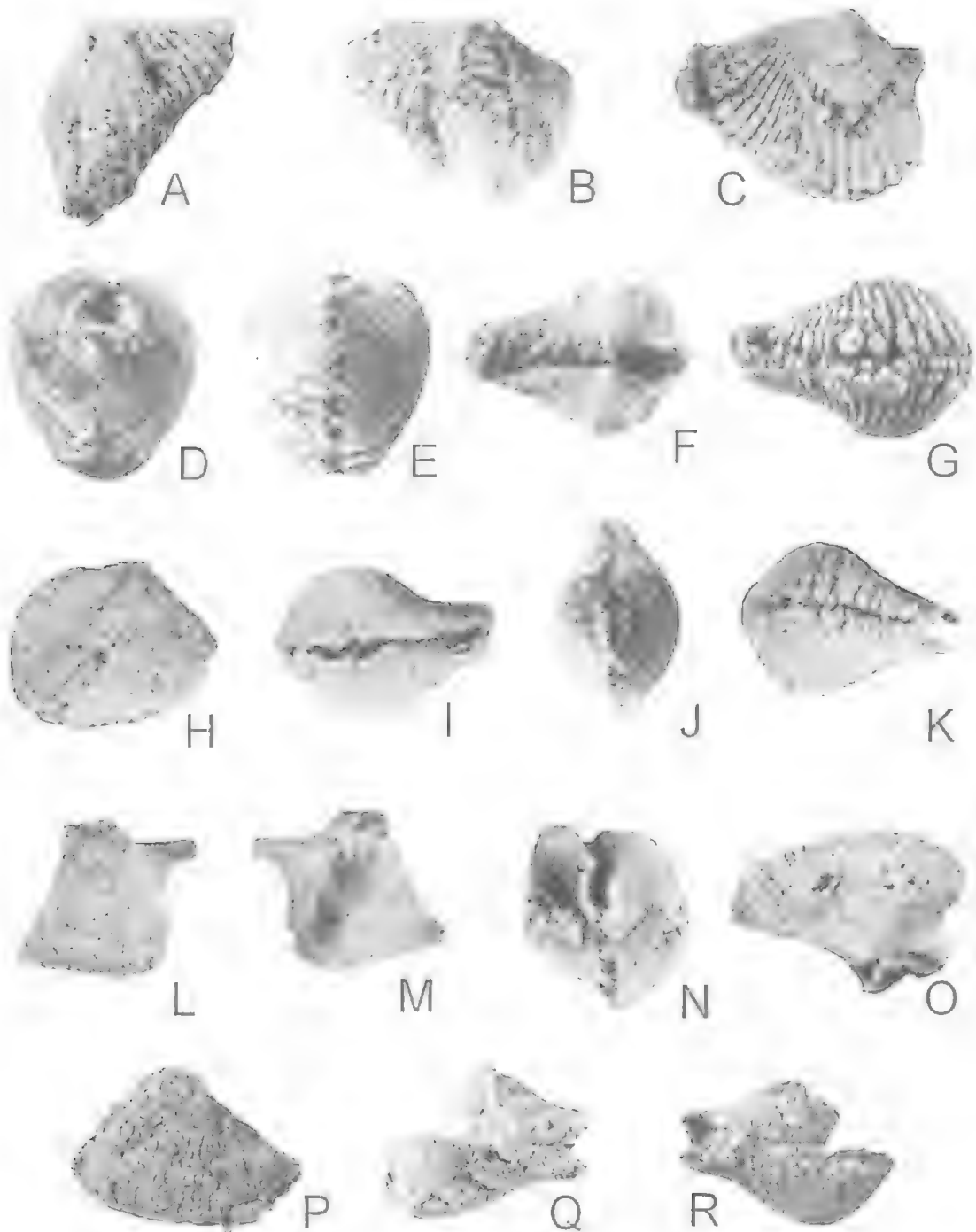


FIG. 5. A,B, *Conocardium gogoense* Fletcher, 1945. A, QMF36085 right valve, $\times 4$; B, QMF42233 left valve, $\times 4$. C-R, *Conocardium* sp. 2. C-G, QMF37317, $\times 3.2$, right lateral, posterior, anterior, dorsal and ventral views; H-K, QMF37314, $\times 4$ right lateral, dorsal, inclined posterior and ventral views; L, M, QMF37316, $\times 1.6$ left lateral and internal views; N,O, QMF37317 $\times 3$, posterior and right lateral inclined views; was not illustrated P-R, QMF37320, $\times 2.5$, left lateral, dorsal and ventral views.

Conocardium sp. 1
(Fig. 3J-L)

MATERIAL. QMF41330 from the Dongangling Formation, 7km NW of Ertang, Wuxian County, Guangxi Province China; Middle Devonian (Givetian).

DESCRIPTION. Medium sized, tumid, quadrate in outline, 7.3mm high, 7.1mm long, 7.2mm maximum width. Rostrum well below dorsum, projecting from short steep convex posterior face. Gape widening strongly dorsally, with long denticles. Shell reticulate with subequal ribs dominant on anterior face, comarginal lines fine, very numerous. Posterior face with coarse ribs and much finer radial lines. Rostral clefts unknown.

REMARKS. This stout taxon differs from the type species *C. elongatum* (Sowerby) by the shortness of the shell. From *Conocardium sowerbyi*, from the Devonian of Tasmania, it differs in its more tumid shell form. I can find no other records of Middle Devonian rostroconchs from Guangxi.

Conocardium sp. 2
(Fig. 5C-R)

MATERIAL. QMF37315-37320 from QM1 1095, Utting Calcarenite, Utting Gap Bonaparte Gulf Basin, WA; Carboniferous, Viséan.

DESCRIPTION. Shell, medium sized, up to 19mm long 13mm high and 9mm wide, moderately inflated, rostrum prominent, slightly below the hinge axis, gently inclined upwards from the shell margin. Rostral clefts unknown. Anterior gape with weak denticles. Ornament of flattened wide ribs, with comarginal rugae confined to posterior surface.

LITERATURE CITED

- BANKS, M.R. & BURRELL, C.F. 1989. The Gordon Group (Early Ordovician to Early Silurian)-mainly platform carbonates. Geological Society of Australia Special Publication 15: 201-212.
- CHAPMAN, F. 1908. A monograph on the Silurian bivalved Mollusca of Victoria. Memoirs of the National Museum of Victoria 2: 1-62.
- COLQUHOUN, G.P. 1995. Early Devonian conodont faunas from the Capertee High, NE Lachlan Fold Belt, southeastern Australia. Courier Forschungsinstitut Senckenberg 182: 347-369.
- COOK, A.G. 1988. Aspects of the lower Kandos Limestone, New South Wales. Unpubl. BSc (Hons) thesis, University of Wollongong, NSW.
- CRESSWELL, A.W. 1893. Notes on the Lilydale Limestone. Proceedings of the Royal Society of Victoria N.S. 5: 38-46.
- ETHERIDGE, R. 1881. Notes on a collection of fossils from the Palaeozoic rocks of New South Wales. Journal and Proceedings of the Royal Society of New South Wales 14: 247-258.
1883. A description of the remains of trilobites from the Lower Silurian rocks of the Mersey River District, Tasmania. Papers and Proceedings of the Royal Society of Tasmania 1882: 150-163.
- FLETCHER, H.O. 1943. The genus *Conocardium* from Australian Palaeozoic rocks. Records of the Australian Museum 21: 231-243.
- JELIĆ, J.S., SIMPSON, A., MAWSON, R. & TALENT, J.A. 1993. Biostratigraphic summary. Pp. 239-245. In Withnall, I.W. & Lang, S.C. (eds) Geology of the Broken River Province, north Queensland, Queensland Geology 4. (Department of Minerals and Energy: Brisbane).
- KONINCK, L.G. De. 1876. Recherches sur les fossiles paléozoïques de la Nouvelle-Galles du Sud (Australie). Mémoires de la Société Royale des Sciences de Liège. Deuxième série. 6: 1-135.
- PEMBERTON, J.W., COLQUHOUN, G.P., WRIGHT, A.J., BOOTH, A.N., CAMPBELL, J.C., COOK, A.G. & MULLISTEED, B.D. 1994. Stratigraphy and depositional environments of the northern Capertee High. Proceedings of the Linnean Society of New South Wales 114: 105-134.
- PLAYFORD, P.E. & LOWRY, D.C. 1966. Devonian reef complexes of the Canning Basin, Western Australia. Geological Survey of Western Australia Bulletin 118: 1-150.
- POJETA Jr, J. 1979. Geographic distribution of Cambrian and Ordovician rostroconch mollusks. In Gray, J. (ed.) Historical biogeography, plate tectonics, and the changing environment. (Oregon State University Press: Corvallis).
- POJETA Jr, J., GILBERT-TOMLINSON, J. & SHERGOLD, J.H. 1977. Cambrian and Ordovician rostroconch mollusks from northern Australia. Bureau of Mineral Resources, Geology and Geophysics Bulletin 171: 1-54, pls 1-27.
- POJETA, J. & RUNNEGAR, B. 1976. The paleontology of rostroconch mollusks and the early history of the phylum Mollusca. United States Geological Survey Professional Paper 968: 1-88, pls 1-54.
- ROBERTS, J.R. 1971. Devonian and Carboniferous brachiopods from the Bonaparte Gulf Basin, northwestern Australia. Bureau of Mineral Resources Geology and Geophysics 122: 1-319.
- TALENT, J.A. 1956. Devonian brachiopods and pelecypods of the Buchan Caves Limestone Victoria. Proceedings of the Royal Society of Victoria NS. 68: 1-56.
- TALENT, J.A. & PHILIP, G.M. 1956. Siluro-Devonian Mollusca from Marble Creek, Thomson River, Victoria. Proceedings of the Royal Society of Victoria n.s. 68: 57-72.
- TASSILLI, C.B. 1982. Some Siluro-Devonian rostroconch mollusks from southeastern Australia. Records of the Queen Victoria Museum 79: 1-11.

HERPETOLOGICAL 'FOREIGNERS' ON NORFOLK ISLAND, AN EXTERNAL TERRITORY OF AUSTRALIA. *Memoirs of the Queensland Museum* 46(2): 408. 2001:-

'Biotas of islands, especially oceanic islands, characteristically differ from continental biotas in four ways. They are relatively impoverished, unsaturated, and disharmonic, and they harbor a disproportionately high number of endemic species. This last trait – high endemism – means that island species are crucially important to global biodiversity, while the first 3 traits are often seen as causing island species and communities to be particularly fragile. This is the island dilemma – great biodiversity, much of it not found elsewhere, but great danger' (Simberloff, 2000). The Norfolk group (29°02'S 167°57'E) is a volcanic and sedimentary island cluster 1,367km east of Australia, 772km northeast of New Zealand and 675km south of New Caledonia (Schodde et al., 1983). The extant and extinct biotas of these islands are highly endemic and, predictably, have affinities with those from Australia, New Zealand and New Caledonia/the tropical Pacific (Holloway, 1977; Cogger et al., 1983; Schodde et al., 1983).

Reptiles are scant on the Norfolk group. Two species – a gecko, *Christinus guentheri* (Boulenger, 1885) and a skink, *Oligosoma lichenigera* (O'Shaughnessy, 1874) – occur there. Populations referred to these species occur also on the Lord Howe I group, 900km to the east. Whether these taxa are conspecific with the Norfolk populations is uncertain. Norfolk and Lord Howe populations are known to be distinct to 'some degree' (Cogger et al., 1993). Neither *C. guentheri* nor *O. lichenigera* occurs on the main island (Norfolk) in the former group, although *C. guentheri* is reported from Holocene deposits there (Cogger et al., 1983). In the Norfolk group, *C. guentheri* occurs on Phillip I., Nepean I., Moo'oo Rock and Bird Rock. *O. lichenigera* is known from only Phillip I. Both species are reputed to have 'disappeared' from Norfolk I. due, largely, to the introduction (by Polynesian colonists some 900 ybp) of *Rattus exulans*. Reputed declines of populations of both species on Phillip I. have been attributed to massive habitat destruction there, by introduced rabbits, pigs and goats (Cogger et al., 1993). Both *C. guentheri* and *O. lichenigera* are classed 'endangered' (Cogger et al., 1993). Should the Norfolk group populations prove to be distinct from those on the Lord Howe group, the already narrow occurrences of each will be halved and their vulnerability to extinction will increase concomitantly. Frogs and other amphibians are unknown in both fossil and modern records for all islands in the Norfolk group.

Given the uniqueness of the Norfolk group's biota and its high vulnerability to further population declines and extinction, we report a series of reptile and amphibian specimens recently introduced to the main island of the Norfolk group. Specimens of 3 coloniser species have been found either on the island or in cargo for the island on a vessel anchored there, since 1998:

Bufo marinus (Linnaeus, 1754). Cane Toad QMJ74062 ♀; near the Colonial Hotel, Burnt Pine, Norfolk I.; Neil Tavener, mid 1999. This specimen was collected following its sighting by hotel staff and by a visitor from Cairns, NEQ.

Litoria caerulea (White, 1790) Green Tree Frog. QMJ74063, near watertank by workshops, Norfolk I. airport. Charles Buffett, 18 Nov. 1999; QMJ74064 'Pot Pourri' shop. Burnt Pine, Norfolk I., Joan Kenny, early 1998; QMJ74065 in pallet of airfreight from Brisbane, SEQ, Norfolk I., ca 1998.

Hemidactylus frenatus Duméril & Bibron, 1836. QMJ74060 Norfolk I., on a drum of telephone cable imported to the island from Australia, via Yamba, ca June 2000, Glen Williams and Tony Grant, 13 Sept., 2000. QMJ74061, amongst timber on board MV *Southern Moana* anchored at Norfolk I. to discharge cargo. Neil Tavener, early 2000. MV

Southern Moana serves Auckland, Norfolk I., Raratonga, (Cook Islands) and, occasionally, docks in Aitutaki (Cook Islands) and Niue Island. These are the first specimens of herptiles foreign to the Norfolk I. group to be recorded there. Cogger et al. (1983) conducted detailed herpetological surveys on all islands in the group and reported the presence of only *C. guentheri* and *O. lichenigera*. Since that time, no other herpetological specimens from the Norfolk group have been added to the collections of the Australian Museum, Sydney (R. Sadlier, pers. comm.).

B. marinus, *L. caerulea* and *H. frenatus* are aggressive and highly successful colonisers elsewhere. *B. marinus*, introduced to a handful of sugar cane-growing districts in coastal Queensland between 1935 and 1938, now occurs from the Mann R., NT, to northeastern New South Wales (Covacevich & Archer, 1975; R. Alford, pers. comm., October, 2000). *L. caerulea* is native to, common, and widespread in northern and eastern Australia. It adapts exceptionally well to urban areas and to agricultural and grazing lands and is known to travel easily with produce and building material. *H. frenatus* is a recent, very successful coloniser of Australia. It is presumed to have entered Australia with cargoes from ports in Asia and/or the Pacific Islands. Specimens were observed in Australia first in Darwin in 1964, but *H. frenatus* is believed to have entered Australia before then, Horner, pers. comm.; 2000; Wilson, 2000. *H. frenatus* is now widely distributed in and near Queensland ports from Cooktown to the Gold Coast (Queensland Museum records) and has been reported recently from Adelaide, SA (M. Hutchinson, pers. comm., September, 2000). In Brisbane, SEQ, *H. frenatus* has been extraordinarily successful. Earliest Brisbane specimens were collected on the wharves in 1983 (QMJ41978). This species is now probably the most common gecko in Brisbane, having moved from wharves, to inner city buildings and parks, to suburban homes/gardens with what appears to be astonishing success.

Discovery of specimens of these 3 species on the Norfolk group has implications for its future. All are highly successful in new, especially disturbed, habitats; thrive in the subtropics; and, if they gain even a tiny 'foothold' on the island/s, will become conspicuous elements of the Norfolk fauna, already dominated by species introduced by Europeans: one species (*H. frenatus*) may have the potential to 'out compete' the gecko (*C. guentheri*) endemic to the group; and two species (*B. marinus*, *L. caerulea*) will fill the present vacant amphibian/riparian niche on Norfolk I. on a massive scale.

Literature Cited

- COVACEVICH, J. & ARCHER, M. 1975. The distribution of the cane toad, *Bufo marinus*, in Australia and its effects on indigenous vertebrates. *Memoirs of the Queensland Museum* 17: 305–310.
- COGGER, H.G., CAMERON, E.E., SADLIER, R.A. & EGILIER, P. 1993. The Action Plan for Australian Reptiles. (Australian Nature Conservation Agency: Canberra).
- COGGER, H., SADLIER, R. & CAMERON, E. 1983. The terrestrial reptiles of Australia's island territories. Special Publication II (Australian National Parks and Wildlife Service: Canberra).
- HOLLOWAY, J.D. 1977. The Lepidoptera of Norfolk Island: their biogeography and ecology. (Dr W. Junk B.V.: The Hague).
- SCHODDE, R., FULLAGAR, P. & HERMES, N. 1983. A review of Norfolk Island birds: past and present. Special Publication 8. (Australian National Parks and Wildlife Service: Canberra).
- SIMBERLOFF, D. 2000. Extinction – proneness of island species causes and management implications. *The Raffles Bulletin of Zoology* 48(1):1–9.
- WILSON, S. 2000. Geckos. The eyes have it. *Australian Geographic* 59: 72–89.
- J.A. Covacevich¹, A.F. Buffett², P.J. Couper¹ & A.P. Amey¹.
¹Queensland Museum, PO Box 3300, South Brisbane 4101;
²Health and Quarantine, Kingston, Norfolk Island 2899; 12 May 2001

AUSTRALIAN SPECIES OF ARISTEIDAE AND BENTHESICYMIDAE (PENAEOIDEA: DECAPODA)

W. DALL

Dall, W. 2001 06 30: Australian species of Aristeidae and Benthescymnidae (Penaeoidea: Decapoda). *Memoirs of the Queensland Museum* 46(2): 409-441. Brisbane. ISSN 0079-8835.

Twelve species of Aristeidae from Australian seas, representing all genera in the family, have been identified (*indicates new records). *Aristacomorpha foliacea*, *Aristacopsis edwardsiana*, **Aristeus mahahissae*, *A. virilis*, *Austropenaeus nitidus*, **Hemipenaeus carpenteri*, **Hepomadus tener*, **Parahepomadus vauhani*, **Plesiopenaeus armatus*, **P. coruscans*, **Pseudaristeus kathleenae*, **P. sibogae*. (*Aristeus semidentatus* has also been recorded from Australia, but its identity could not be confirmed in existing museum collections). In the Benthescymnidae ten species have been identified: *Benthescymnus investigatoris*, *B. urinator*, *Gennadas haueri*, *G. capensis*, *G. gilchristi*, *G. incertus*, *G. kempi*, *G. propinquus*, *G. scutatus*, *G. tinayrei*, plus a new subspecies *Benthescymnus urinator howensis*. Definitions of the 2 families and the genera represented, with keys, are included. Keys to the Indo-West Pacific species are given, together with diagnoses of the Australian species. Zoogeography of the 2 families is discussed briefly □ Indo-West Pacific. *Aristeidae*, *Benthescymnidae*, *Australia*, *diagnoses*, *distribution*, *zoogeography*.

W. Dall, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia;
1 November 2000

Up to the late 19th century all penaeoid decapods were included in the Penaeidae. It was recognised, however, that there were major differences between some groups and Wood-Mason (1891) identified 3 distinct deep-water groups in the Penaeidae: Aristaeina, Benthescymnina and Solenocerina. Later, the Aristaeina was raised to family status to include the Aristaeinae, Benthescymninae and Solenocerinae. These 3 sub-families have been raised to family level within the Penaeoidea (Pérez Farfante & Kensley, 1997). Thus there are now 5 families within this super-family, distinguished as follows.

KEY TO THE FAMILIES OF THE PENAEOIDEA

1. Postorbital* spine present Solenoceridae
Postorbital spine absent 2
2. Third to fifth pleopods uniramous. Sicyoniidae
Third to fifth pleopods biramous 3
3. Dorsal rostral teeth plus postrostral teeth 0-2, rarely 3; rostrum truncate, deep and ranging from short of, to barely exceeding the cornea; adrostral carina absent; antero-ventral carapace usually emarginate Benthescymnidae
Dorsal rostral teeth plus postrostral teeth more than 2; rostrum usually well exceeding the cornea; adrostral carina usually present; antero-ventral region of the carapace not deeply emarginate 4
4. Upper antennular flagellum much shorter than the lower and attached laterally to the third segment of the antennular peduncle; prosartema reduced to a setose knob. Aristeidae

Upper antennular flagellum of similar length to the lower and attached apically to the third segment of the peduncle; prosartema well developed and foliaceous Penaeidae

* In some solenocerid genera this could be identified as a postantennal spine. In the Aristeidae *Parahepomadus* has a postantennal spine, but the antennular flagella and long rostrum with only three teeth readily distinguish it from the Solenoceridae.

Twentyseven species of Solenoceridae have been identified from Australian seas (Dall, 1999), but although several species of Aristeidae are common in deeper water commercial prawn trawls, only 13 Australian species are described in this paper. The Benthescymnidae are small and delicate and few were in the collections of Australian museums until the advent of extensive investigations using mid-water trawls, which collected 8 *Gennadas* species from Australian seas. While the Solenoceridae largely inhabit the continental slope, the Aristeidae are mostly found from the lower slope into deeper water, exceptionally down to 5,000m. Some Benthescymnidae are mesopelagic or bathypelagic, others are benthic, often at depths below 1,000m.

Key taxonomic papers on the Aristeidae and Benthescymnidae are by Crosnier (1978, 1985), Crosnier & Forest (1973), Kensley (1971), Kensley et al. (1987), Kikuchi & Nemoto (1991), Pérez Farfante (1973, 1987), Pérez Farfante & Kensley (1997). Most of these publications and others describe specimens from outside

Australian waters. This paper therefore attempts to cover the Australian species in sufficient detail to facilitate their identification by non-specialists. Definitions are given of the families and genera, with keys. Species keys include known Indo-West Pacific species, because it is likely that, in the future, some additional species will be found in Australian seas. The species diagnoses and figures are from specimens in the collections of the Australian (AM), Northern Territory (NT), Queensland (including Museum of Tropical Queensland) (QM), Tasmanian (TMH) and Victorian (MV) Museums and the CSIRO Marine Laboratories, Hobart. Generally synonymies are restricted to primary and key references, especially where the commoner species, such as *Aristaeomorpha foliacea* have a very extensive synonymy. General taxonomic features of the carapace and appendages are identified in Grey et al. (1983) or in Dall et al. (1990). The special taxonomic features of the Solenoceridae Dall (1999) are also applicable to the Aristeidae and Benthescymidae, except for the nomenclature of the anterior branchiostegal region. In the Benthescymidae the anterior end of the branchiostegal emargination is often marked by an angular projection, the infra-antennal angle. Also, all members of both families have, near or on the margin of the carapace, a branchiostegal spine, which is continuous with a carina of varying length. It is similar to the hepatic carina of other families, particularly when it extends past the lower end of the cervical sulcus. In many other species it stops well short of this region and could equally be called a branchiostegal carina. For the sake of uniformity it will be described here as an hepatic carina.

Length. Except when scale bars are included in figures, lengths are carapace length (CL) i.e. distance between the posterior rim of the orbit

and the midline of the posterior rim of the carapace.

SYSTEMATICS

Superfamily PENAEOIDEA Family ARISTEIDAE Wood-Mason, 1891

- Aristaeina* Wood-Mason, 1891: 278.
Aristaeinae Alcock, 1901: 27; Ramadan, 1938: 36; Kubo, 1949: 193.
Aristeinae Bouvier, 1908: 6, 13; Balss, 1957: 1516; Crosnier, 1978: 14.
Aristeidae Crosnier, 1978: 14; De Freitas, 1985: 3; Squires, 1990: 20; Pérez Farfante & Kensley, 1997: 32.
Aristaeidae Grey et al., 1983: 14; Dall et al., 1990: 58.

DIAGNOSIS. Rostrum usually elongate, apparently sexually dimorphic in some genera, being shorter in adult ♂♂; with 3 or more dorsal teeth, without ventral teeth. Antennal and branchiostegal spines always present, postorbital and pterygostomial spines absent; postantennal and hepatic spines rarely present, cervical sulcus variable, sometimes reaching the dorsum, sometimes weak and restricted to the lateral surface of the carapace; postcervical sulcus sometimes present. Abdominal somites 4-6 always carinate, somite 3 sometimes carinate; telson apically acute with 3 or 4 pairs of movable lateral spines. Optic peduncle with a mesial tubercle, optic scale absent. Prosartema reduced to a setose boss; antennular flagella unequal, the dorsal flagellum very short and flattened and inserted proximally into the third segment; ventral flagellum long and sexually dimorphic in some genera; maxillulary palp unsegmented. Exopods on all maxillipeds, present or absent on pereopods; pereopods 4 & 5 usually more slender and longer than pereopod 3. Pleopods well developed, sometimes longer than the carapace. Petasma simple, open; second male pleopod with appendix masculina consisting of inner and outer projections (sometimes referred to as appendix

TABLE 1. Distribution of branchiae and epipods on thoracic somites of Aristeidae. * s = small; r = rudimentary.

Genus	Pleurobranchs Somites 3-8	Arthrobranchs Somite 1	Arthrobranchs Somite 2	2 Arthrobranchs Somites 3-7	Podobranchs Somites 2-5	Epipods Somites 1-7
<i>Aristaeomorpha</i>	+(3 s)*	s	s, l	+	+(also 6)	+
<i>Aristaeopsis</i>	+	l	s, l	+	+(also 6)	+
<i>Aristeus</i>	+(s or r, 3-7)	l	s, l	+	+	1-6 only
<i>Austropenaeus</i>	+	l	s, l	+	+(also r on 6)	+
<i>Hemipenaeus</i>	+	l	s, l	+	+	+(r on 7)
<i>Hepomadus</i>	+	l	r, l	+	+	+(r on 7)
<i>Parahepomadus</i>	+	l	s, l	+	+	+(s on 7)
<i>Plesiopenaeus</i>	+	s	s, l	+	+(also 6)	+(s on 7)
<i>Pseudaristeus</i>	+	r	s, l	+	+	1-6 only

interna and appendix masculina, respectively) and no distolateral projection. Thelycum open, seminal receptacle deep; thoracic somite 7 with a shield-like median plate. The arrangement of branchiae and epipods of the genera of the Aristeidae are listed in Table 1.

REMARKS. Pérez Farfante (1987) concluded that the relative length of the rostrum in some genera is size dependent as well as being sexually dimorphic. The prevailing view is that this is true sexual dimorphism and not due to an earlier breakage of this structure, which is often more slender in ♂♂, followed by regeneration of a new tip. (Some adult ♀♀ also show evidence of such a regeneration).

The family as now defined, is very homogeneous and consists of 9 genera, all of which have been recorded from Australian seas. *Aristeomorpha* stands a little apart from the other genera: with 6-11 fairly evenly spaced dorsal rostral teeth; basicerite with a prominent spine (like that in other penaeoid families); petasmal halves diverging distally and ventral costa attached along its length; and thoracic 8 sternite of the thelycum with a short rounded median prominence. The remainder are similar in appearance and some are difficult to distinguish, sometimes relying on rather minor features of the cephalothorax or abdomen. For example, the rudimentary exopods (Fig. 1) which separate 2 groups of 3 genera each are often difficult to detect. Unfortunately, better criteria do not seem to exist. Also, the trend in taxonomy of the Aristeidae has been to create small genera. Thus of the 9 genera 4 are monospecific, 2 contain 2 species and 1 includes 3. A revision of the family is perhaps needed at this stage and certainly before any new genera are created.

KEY TO GENERA OF THE ARISTEIDAE

1. Hepatic spine present 2
Hepatic spine absent 3
2. Three dorsal rostral teeth, including the postrostral (epigastric) tooth. *Hepomachus*
More than three dorsal rostral teeth, including the postrostral tooth. *Aristeomorpha*
3. Postantennal spine present *Penaeus*
Postantennal spine absent 4
4. Exopods absent from all pereopods 5
Exopods (usually reduced or rudimentary, Fig. 1) present on all pereopods 7
5. A sub-distal meral spine present on pereopods 1 & 2; scaphocerite in male not modified. 6
No meral spines on pereopods 1 & 2; scaphocerite in male distally elongate. *Aristeopsis*

6. Cervical sulcus distinct and extending to the dorsum of the carapace; postcervical sulcus present. *Pseuduristrix*
Cervical sulcus reduced to a very short sulcus in the hepatic region; postcervical sulcus absent *Aristeus*
7. Abdominal somite 3 carinate; epipod on pereopod 4 rudimentary *Hemipenaeus*
Abdominal somite 3 not carinate; epipod on pereopod 4 large. 8
8. Podobranchia on pereopod 3 rudimentary; carinae on the carapace weak; ventral antennular flagellum and dactyl of the third maxilliped modified in the male *Antropenaeus*
Podobranchia on pereopod 3 large; carinae on the carapace well defined; ventral antennular flagellum and dactyl of the third maxilliped not modified in the male *Plesiopeneus*

Aristeomorpha Wood-Mason, 1891

Penaeus Risso, 1827: 69 [part]; H. Milne-Edwards, 1837: 418 [part].

Aristeus Bate, 1881: 189; 1888: 317 [part].

Aristeomorpha Wood-Mason, 1891: 286; Anderson & Lindner, 1943: 301; Kubo, 1949: 200; Crosnier, 1978: 52; Hayashi, 1983b: 280; de Freitas, 1985: 15; Liu & Zhong, 1986: 33; Pérez Farfante & Kensley, 1997: 33.

Aristeomorpha Senna, 1903: 268; Bouvier, 1908a: 52; Ramadan, 1938: 53.

DIAGNOSIS. Integument finely pubescent, with a pair of large ventral photophores on the thoracic and abdominal somites with a pattern of smaller photophores on the ventral surface, the scaphocerites, external uropods and most of the other appendages. Rostrum reaching well beyond the scaphocerite in females and juveniles, usually shorter than the antennular peduncle in adult ♂♂; with 5-9 dorsal teeth in all; adrostral carina reaching between the first and second rostral teeth; postrostral carina low and reaching about half the carapace. Antennal and branchiostegal spines present, the latter on the margin of the carapace with a carina extending almost to the hepatic spine; hepatic spine large,

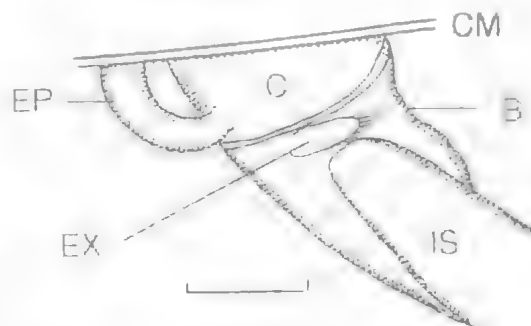


FIG. 1. Rudimentary exopod on basis of pereopod 3 of *Antropeneus nitidus* (de Man, 1911). AM P55936. 34°49'S 151°14'E. 1225 m. ♀. 33 mm. B, basis; C, coxa; Ep, epipod; Ex, rudimentary exopod; IS, ischium; CM, margin of carapace. (Scalebar = 1 mm).

cervical sulcus reaching about halfway to the dorsum. A deep sulcus extends from a shallow emargination below the branchiostegal spine to its junction with the hepatic sulcus, which turns ventrad at the mid-carapace; hepatic carina short and blunt; branchiocardiac carina prominent, the sulcus shallow, the carina extending from the divergence of the hepatic sulcus almost to the posterior margin of the carapace. A low carina, sometimes barely visible, on the posterior two thirds of abdominal somite 3, 4-6 fully carinate, all 4 somites ending in a sharp spine. Telson with 4 pairs of small lateral movable spines. Eye large; stylocerite reaching about 0.75 the first segment of the antennular peduncle. Dorsal antennular flagellum flattened with terete tip, slightly longer than the third antennular segment, ventral flagellum long, not modified in the male. Lateral spine of the scaphocerite at about 3/4 the length of the lamella; scaphocerite not modified in the male. Pereopods without exopods or ischial and meral spines; pereopod 3 with a large podobranch. Petasma simple with diverging apices; thelycum with a deep hemicylindrical receptacle, formed by a shield-like anterior plate on thoracic somite 7, the rounded apex directed anteroventrally, the coxae of the pereopod 5 and a rounded median boss on somite 8.

REMARKS. Armature of the rostrum sets *Aristaeomorpha* apart within the family. The 2 species, *A. foliacea* (Risso, 1827) and *A. woodmasoni* Calman, 1925, are distinguished by the relative depths of the pterygostomian area, the length/depth ratios being 3.5-4.0 and <2.5, respectively. Other features are minor (relative lengths of the uropods and dactyls of the fourth and fifth pereopods). Barnard (1950) pointed out that Kemp & Sewell (1912) could find no differences in the petasmas and thelyca of the 2 species. *A. woodmasoni* has so far been recorded only from Indian waters and its specific status needs to be re-examined as *A. foliacea* has been recorded from the Maldiv Islands, Sri Lanka, Indonesia and surrounding seas.

While *Aristeus* and possibly other members of this family have photophores, at least on the appendages, *A. foliacea* appears to be the most luminescent (Crosnier, 1978: 57, fig 23e-f, for

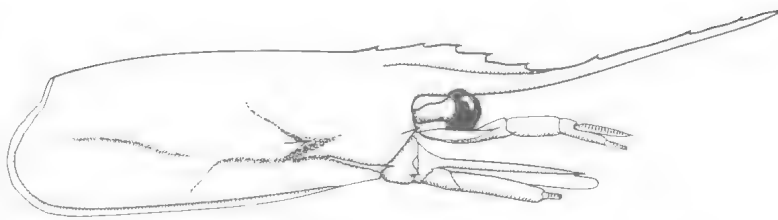


FIG. 2. *Aristaeomorpha foliacea* (Risso, 1827) QMW10091, 26°20'S, 153°53'E, 300m, ♀, 42mm.

full description). It is widely distributed (Crosnier, 1978 listed 99 references in his 'Bibliographie partielle') and occurs in deeper-water prawn fisheries, including SE Australia.

Aristaeomorpha foliacea (Risso, 1827) (Fig. 2)

Penaeus foliacea Risso, 1827: 69, pl. 2, fig. 6; Milne-Edwards, 1837: 418; Miers, 1878: 307.
Aristeus rostridentatus Bate, 1881: 189; 1888: 317, pl. 51.
Aristaeomorpha Giglioliana Wood-Mason, 1892: pl. 2, fig. 2.
Aristaeomorpha foliacea (see Crosnier, 1978 for bibliography prior to 1976); Crosnier, 1978: 54, fig. 23; 1984: 21; 1985: 861; 1989: 42; 1994b: 369; Hayashi, 1983b: 280, fig. 53; Grey et al., 1983: 46, pl. 1; de Freitas, 1985: 16, fig. II-7; Liu & Zhong, 1986: 33, figs 12, 13; Kensley et al., 1987: 279; Hanamura, 1989: 51.

MATERIAL. QM W10091, 26°20'S 154°E, 300m, ♂, 43mm, 2 ♀, 42, 43mm; QMW11428, 23°46'S 153°E, 550m, ♂, 40mm, 3 ♀, 44, 44, 46mm; QMW14351, 26°30'S 153°45'E, 390m, ♂, 43mm, ♀, 40 mm; QMW15292, 28°S 153°54'E, 550m, 2 ♂, 28, 35mm, ♀, 42mm.

DIAGNOSIS. Apart from the differences in pterygostomian depths of the 2 species noted above, the genus diagnosis is also the specific definition.

Colour. Uniformly deep pink to wine red (colour plate in Grey et al., 1983).

DISTRIBUTION. E Australia and Tasmania, 18°-42°42'S, the western approaches to Bass Strait, Great Australian Bight, Arafura Sea, 8°34'S 131°E, through the Northwest Shelf to 28°S on the west coast; 250-700 m on mud to muddy sand. Thus it is likely to occur at these depths all round Australia. Known range: cosmopolitan, Indian Ocean from SW and E Africa, Madagascar, Réunion, Maldiv Islands, Sri Lanka, Indonesia, Philippines, China Sea, Japan, Australia, New Zealand, New Caledonia, Wallis and Futima Islands, Fiji, W Atlantic Ocean, from Massachusetts to Venezuela, Mediterranean Sea, E Atlantic Ocean from Bay of Biscay to Rio de Oro. Depth range 170-810m,

although exceptionally caught up to 61m. Crosnier (1978) suggested that there may be a diurnal migration from deep to shallower water at night.

Aristaeopsis Wood-Mason, 1891

Aristaeopsis Wood-Mason, 1891: 282; Bouvier, 1908: 61; Burkenroad, 1936: 94 [part]; Crosnier, 1978: 86; Pérez Farfante & Kensley, 1997: 36.

Plesiopenaeus Faxon, 1895: 199 [part]; Milne-Edwards & Bouvier, 1909: 200 [part]; Burkenroad, 1936: 94 [part]; Ramadan, 1938: 49; Barnard, 1950: 621 [part]; Crosnier, 1978: 85 [part]; Squires, 1990: 41. (non *Plesiopenaeus* Bate, 1881).

Aristaeus (*Plesiopenaeus*) Alcock, 1901: 35 [part].

Aristeopsis de Man, 1911: 6.

DIAGNOSIS. Integument glabrous, carapace firm. Rostrum with unarmed tip upcurved, as long as the carapace in ♀♀ of 30mm CL, decreasing to around 0.55 of the carapace at 62mm CL, not sexually dimorphic although often damaged in ♂♂; with 3 dorsal rostral teeth; adrostral carina not quite reaching the first rostral tooth; postrostral carina low, but reaching about 0.8-0.9 the carapace. Antennal spine with a well-defined carina; hepatic spine absent; branchiostegal spine on the margin of the carapace and continuous with a prominent carina running almost to the branchiocardiac carina; hepatic sulcus deep, occupying three-quarters the posterior part of the carina and descending to the submarginal carina. Gastro-orbital carina prominent, extending from just behind the orbit almost to the upper end of the prominent cervical carina; cervical sulcus deep in the lower part, but barely defined in the upper half, where it sometimes meets the dorsum; branchiocardiac carina and sulcus prominent and reaching the posterior margin of the carapace; two irregular carinae running from the cervical carina to the branchiocardiac sulcus. A dorsal carina beginning on the posterior quarter of abdominal somite 2 and continuing to somite 6, abdominal somites 3-6 each with a sharp carina and each ending in a prominent spine; telson with four pairs of small movable spines. Dorsal antennular flagellum short, flattened; ventral flagellum long, tapering and not modified in the male; scaphocerite in the adult male with an elongate distal projection, ovate in cross section, and sub-equal in length to the lamellar part. Pereopods without exopods, pereopod 3 with podobranchia;

pereopods 1 & 2 without distal movable ischial and meral spines. Petasma with dorsal lobule and median lobes of similar length, the ventral costa forming a projecting median hook. Thelycum with an acute anteriorly pointed prominence on thoracic somite 7, the posterior part forming a rounded hollow; eighth somite with a bluntly pointed median prominence. Uniformly scarlet to deep crimson

REMARKS. *Aristaeopsis* was originally created for *Penaeus edwardsianus* by Wood-Mason & Alcock (1891b), but Faxon (1895) synonymised it with *Plesiopenaeus* Bate, 1881 and this usage has persisted for most of the 20th century. Burkenroad (1936) recognised 4 species of *Plesiopenaeus* (*P. edwardsianus*, *P. armatus*, *P. coruscans* and *P. nitidus*). Although accepting this classification, Crosnier (1978, table 11) listed a number of differences between *P. edwardsianus* and *P. nitidus* and the other 2 species. For *P. edwardsianus* the most important of these are lack of exopods on all pereopods; a dorsal carina and posterior spine on abdominal somite 3; the modified scaphocerite in ♂; absence of movable distal meral spines on pereopods 1 & 2. Pérez Farfante & Kensley (1997) considered these differences merited the resurrection of *Aristaeopsis* (feminine gender) which thus contains only *A. edwardsiana*. *Plesiopenaeus edwardsianus* has been extensively cited in the literature (Crosnier, 1978 listed 50 references) and because of long familiarity the general recognition of *A. edwardsiana* will no doubt take some time.

Aristaeopsis edwardsiana (Johnson, 1867) (Fig. 3)

Penaeus Edwardsianus Johnson, 1867: 897.

Aristeus Edwardsianus Miers, 1878: 308, pl. 17, fig. 3.

Aristeus corulinus Bate, 1888: 32, fig. 10.

Aristaeopsis Edwardsiana Wood-Mason & Alcock, 1891b: 283, figs 8-9; Wood-Mason, 1892: pl.1, figs 1,2; Alcock 1899.

Aristaeopsis edwardsiana Alcock & Anderson 1894: 147; Pérez Farfante & Kensley 1997: 37, fig. 7.

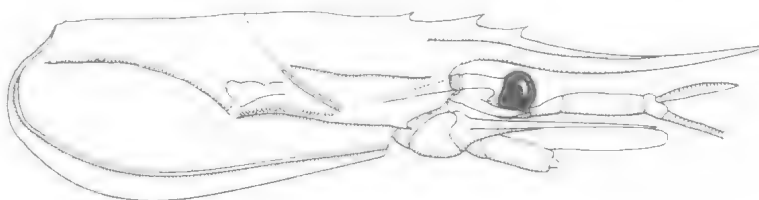


FIG. 3. *Aristaeopsis edwardsiana* (Johnson, 1867) AMP26776, 33°40'S, 151°56'E, 732m. ♀, 45mm.

Plestipenaeus edwardsianus Faxon 1895 (for full synonymy to 1974 see Crosnier, 1978: 88); Crosnier, 1978: 88, figs 31a-c, 32a-c, 33a; Kensley et al. 1987: 281; Hayashi 1983c: 368, fig. 59; Liu and Zhong 1986: 43, fig. 17; Crosnier 1985: 863; 1994b: 369; de Freitas 1985: 20, fig. 2-9; Grey et al. 1983: 38, pl. 2.

MATERIAL. AM P26776, 33°40'S 152°E, 732m, 2♂, 42, 53mm, 10♀, 30-63mm, QMW 11307, 24°S 153°E, 550m, 2♀, 38, 77; QMW11461, 23°34'S 153°E, 650m, ♂ 48mm, 2♀ 64, 82mm; QMW15286, 28°S 154°E, 550m, 3♂, 37, 41, 42mm, ♀, 57 mm; QMW15287, 28°S 154°E, 550m, 3♂, 42, 44, 46mm, 2♀, 40, 50mm; W15291, 28°S 154°E, 550m, ♂, 38mm.

DIAGNOSIS. As for genus.

REMARKS. *A. edwardsiana* occurs regularly in deep water prawn trawls off the Australian east coast, but at best is only of minor commercial importance. Crosnier (1978) reported that, off Madagascar, at the 700-800 depths preferred by the species, catches were barely 6-8 kg/h.

DISTRIBUTION. East coast of Australia, 17°-34°S, Arafura Sea 8°S 132°E, off Rowley Shoals, through the Northwest Shelf to 29°S 113°E; 200-1800 m on muddy substrates. Cosmopolitan, Indo-West Pacific Ocean from South Africa to the Arabian Sea, Bay of Bengal, Andaman Sea, Indonesia, South China Sea, Japan, Australia, Wallis and Futuna Islands; Western Atlantic Ocean from the Grand Banks to French Guiana, Eastern Atlantic Ocean from Portugal to the western Sahara, the Azores, Madeira and Canary Islands, 200-1850m.

Aristeus Duvernoy, 1840

Penaeus Risso, 1816: 96.

Aristeus Duvernoy, 1840: 217; Bate, 1881: 171, 187; 1888: 228, 240, 309; Senna, 1903: 261; Bouvier, 1908: 69; de Man, 1911: 27; Ramadan, 1938: 36; Crosnier, 1978: 60; Hayashi 1983a: 188; Liu & Zhong, 1986: 37; de Freitas, 1985: 3; Pérez Farfante & Kensley, 1997: 39. *Aristaeus* Faxon, 1895: 197; Alcock, 1901: 27; Anderson & Lindner, 1943: 300; Kubo, 1949: 194. *Aristaeus* (*Aristaeus*) Alcock, 1901: 29.

DIAGNOSIS. Integument glabrous or pubescent. Rostrum elongate, reaching well beyond the tip of the antennular peduncle in ♀♀ and young ♂♂, but usually shorter in adult ♂♂; with 3 dorsal teeth. Carapace with an antennal and a

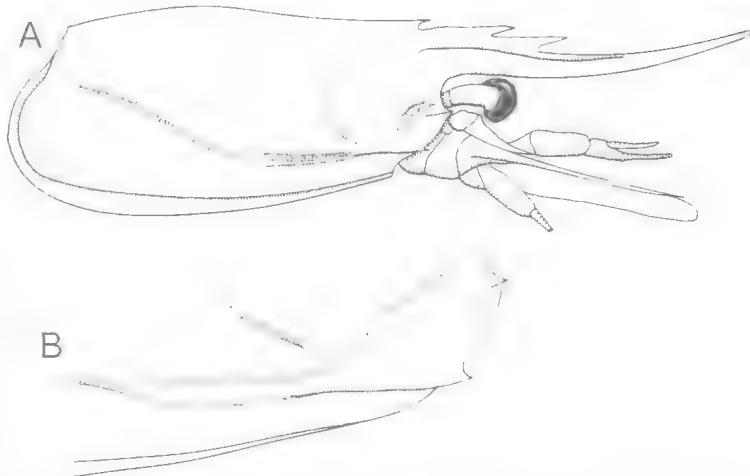


FIG. 4. A, *Aristeus mabahissae* Ramadan, 1938. AMP55934, 34°53'S, 151°15'E, 1116m, ♀, 37mm. B, *A. virilis* (Bate, 1881). NTCR006630, 8°39'S, 132°E, 540m, ♀, 39mm, anterior carapace showing long hepatic carina.

branchiostegal spine, the latter extending back as a carina, other spines absent; cervical sulcus marked only by a short lateral sulcus; branchiocardiac sulcus well-defined, the carina low. Only abdominal somites 4-6 with a distinct dorsal carina; telson with 4 pairs of movable lateral spines, apex acute. Cornea well developed, the peduncle with a prominent tubercle. Dorsal antennular flagellum short, flattened; ventral flagellum long, proximally sinuous in ♂. Pereopods without exopods; pereopods 1 & 2, and sometimes 3 with a movable subdistal meral spine; pereopods 4 & 5 slender; all pereopods with photophores.

Of 8 species known worldwide, 6 occur in the Indo-West Pacific. *A. antennatus* is also an Atlantic species together with *A. antillensis* and *A. varidens*. So far *A. mabahissae* and *A. virilis* have been collected only from Australian waters; *A. semidentatus* is a possible third; *A. antennatus* is listed in the Australian Museum collection, but could not be found at the time of writing and is not described below. Among the Indo-West Pacific species *A. virilis* is readily identifiable because of its finely tomentose integument and pereopods, the spine on the merus of pereopod 3 and a long carina extending posteriorly from the branchiostegal spine. The remaining glabrous species are difficult to distinguish, almost impossible unless the material is in a good state of preservation. Unusually for penaeoids, the genitalia are of limited use for identification; Crosnier (1978) notes that the colouration is identical for *A. antennatus*, *A. mabahissae* and *A.*

TABLE 2. Principal distinguishing features for identification of *Aristeus alcocki*, *A. antennatus*, *A. mabahissae*, *A. pallicauda*, *A. semidentatus*. * P 1 = first pereopod.

Character	<i>A. alcocki</i>	<i>A. antennatus</i>	<i>A. mabahissae</i>	<i>A. pallicauda</i>	<i>A. semidentatus</i>
Length of *P 1 chela/length of carpus	1.15 - 1.25	1.3 - 1.48	1.07 - 1.25	1.41	1.0 - 1.06
Length of P 5 carpus/length of merus	1.08 - 1.18	1.00 - 1.14	0.98 - 1.06	1.24	1.28 - 1.34
Number of photophores on the carpus of P 5	?	65 - 117	4 - 8	36	14 - 21
Number of photophores on the propodus of P 5	?	73 - 98	8 - 13	31	17 - 25
A small spine on the posterior-dorsal edge of the third abdominal somite	Occasionally present	Always with a small spine	Occasionally present	Absent	Absent

semidentatus; the carapace is almost featureless, except for the carination behind the branchiostegal spine. Ramadan (1938) recommends using the ratios between various segments of the pereopods, but often these are not sufficiently different for reliable identification. Crosnier (1978) found that the number of photophores on pereopod 5 could be used as specific characters, at least in a given area; more recently, he has found that they are reliable for most of the Indo-West Pacific (Crosnier, 1994b, & pers. comm.). The red colour of the photophores fades with preservation, but in recently- and well-preserved specimens they may be seen by oblique light as a series of small circular structures. Unfortunately, the photophores are difficult, if not impossible to see in old and poorly preserved material, even if the slender pereopods 5 are present, which is often not the case. Crosnier (1978) recommended that a number of characters be taken in conjunction to distinguish species and the more useful are shown in Table 2. A key is also given, but unless the prawns are fresh, is mostly of value in preliminary identification.

KEY TO THE INDO-WEST PACIFIC SPECIES OF *ARISTEUS*

- 1 Body and pereopods finely pubescent. A subdistal mobile spine near the inferior border of the merus of pereopod 3 (P 3) *A. virilis*
Body glabrous. No mobile spine on the merus of P 3 2
- 2 Ratio length of chela/length of carpus of P 1 approx. 1.0 *A. semidentatus*
Ratio length of chela/length of carpus of P 1 greater than 1.0 3
- 3 A small posterior-dorsal spine on abdominal somite 3; number of photophores on carpus and propodus of P 5 greater than 60 *A. antennatus*
Abdominal somite 3 usually without a spine; number of photophores on carpus and propodus of P 5 less than 60 4
- 4 Ratio length of chela/length of carpus of P 1 greater than 1.3; photophores on carpus and merus of P 5 greater than 20 *A. pallicauda*
Ratio length of chela/length of carpus of P 1 less than 1.3; photophores carpus and merus of P 5 less than 20 *A. mabahissae*

It was not possible to include *A. alcocki* Ramadan, 1938 in the key because the number of photophores on P 5 is not recorded in the literature. So far it appears to be limited to the Gulf of Aden, the Arabian Sea and the Bay of Bengal and thus may not occur in Australian seas. Similarly *A. pallicauda* Komai, 1993 is a rare species recorded only from northern Japan.

Although *A. semidentatus* has been recorded from Australian seas (Kensley et al., 1987), I was unable to confirm this with relevant specimens in the Australian Museum. Some were undoubtedly *A. mabahissae*, others were probably this species and the remainder were unidentifiable as *A. semidentatus*, these 2 species being similar. The criteria listed by Kensley et al. (1987) are in fact identical or very close to those of *A. mabahissae* (Crosnier, 1978) except for the ratio of the lengths of the carpus and merus of pereopod 5. While it is likely that *A. semidentatus* is present in Australian seas, until *bona fide* specimens are collected, it is best to regard existing records as doubtful.

Aristeus mabahissae Ramadan, 1938 (Fig. 4A)

Aristeus mabahissae Ramadan, 1938: 43, figs 2b, 3b, 4a-c; Crosnier, 1978: 65, figs 25c-f, 26c-f; 1984: 22; 1994a: 352, 1994b: 369; Hayashi 1983a: 190, figs 49, 50; Komai, 1993: 22.

MATERIAL. AMP39948, 33°40'S 152°E, 1115m, ♀, 38 mm; AMP39977, 33°S 151°E, 1097m, ♀, 42mm; AMP 55934, 34°53'S 151°E, 1116m, 4♀, 37-44mm; AMP 55938, 35°S 151°E, 1015m, ♂, 20mm, 2♀, 39, 40mm; NT Cr 007070, 29°S 114°E, 880m, 3♀, 39, 43, 53mm; NT Cr 007086, 13°S 122°E, 900m, 2♂, 28, 33mm, 2♀, 34, 41mm; CSIRO, SS/1/91 #44, 27°07'S 112°22'E, 714m, 2♀, 42, 46mm.

DIAGNOSIS. Carapace glabrous. Rostrum in ♀♀ and juvenile ♂♂ variable in length, usually well exceeding the antennular peduncle, the unarmed part slender and upturned, sometimes strongly; often shorter in adult ♂♂; in both sexes with 3 dorsal teeth, the first smaller than the

second and third; adrostral carina ending at the first rostral tooth; postrostral carina reaching about half the carapace. A low gastro-orbital carina above a short, shallow orbito-antennal sulcus; antennal spine extending back as a short antennal carina. A prominent branchiostegal spine on the border of the carapace, extending posteriorly as a sharp carina, which reaches the base of the cervical sulcus and thereafter continues as a blunt prominence, almost meeting the low branchiocardiac carina; hepatic sulcus starting below the cervical sulcus and joining the deep branchiocardiac sulcus, which almost reaches the posterior margin of the carapace. Cervical sulcus restricted to the lateral area of the carapace. A subdistal meral spine on pereopods 1 & 2; pereopod 5 with 4-10 photophores on the carpus and 8-13 on the propodus.

Colour. Variable, the body slightly whitish, with the branchial area, posterior part of the abdominal somites, the extremities of the rostrum and appendages generally rose to rose-orange.

REMARKS. *A. mabahissae* appears to be fairly common in Australian seas. It is easily confused with *A. semidentatus*, but this species may be distinguished by the number of photophores on pereopod 5 (carpus 13-33 and propodus 20-31).

DISTRIBUTION. Eastern Australia 28°-34°S, Western Australia 13°-29°S; 500-1100m. Known range: Madagascar, Maldives, Indonesia, South China Sea, Japan, Australia, Wallis and Futuna Islands, 500-1100m.

***Aristeus virilis* (Bate, 1881)
(Fig. 4B)**

Hemipenaeus virilis Bate, 1881: 187; 1888: 303, pl. 44, fig. 4.
Aristeus tomentosus Bate, 1881: 189; 1888: 307, pl. 49, figs 2, 3, pl. 50.

Aristaeus virilis Faxon, 1895: 198; Alcock, 1901: 30; Kubo, 1949: 194, figs 1, 6, 8, 11, 13, 14, 19, 23, 36, 44, 65, 69, 72, 78, 85, 86.

Aristeus virilis Bouvier, 1908: 70; de Man, 1911: 6, 27; 1913: pl. 2, fig. 6; Ramadan, 1938: 39; Okada et al., 1966: 140, 141, 151, pl. 1, fig. 3; Crosnier, 1978: 61, figs 25a-b, 26a-b; 1984: 21; 1985: 861; 1989: 42; 1994a: 352; Hayashi 1983a: 190, figs 51, 52c,d; de Freitas: 3, fig. 11-1, 1985; Liu & Zhong, 1986: 37, fig. 14; Kensley et al., 1987: 281.

MATERIAL. AMP21683, 29°46'S 154°E, 500m, 3♂, 30, 38, 38mm, 4♀, 34-57mm; QMW11282, 23°S 154°E, 460m, ♂, 39mm, ♀, 55mm; QMW11429, 23°34'S 154°E, 650m, ♀, 48mm; QMW14296, 23°40'S 154°E, 530m, ♀, 38mm; QMW18059, due E Brisbane 28°S, 700-900m, 3♀, 43, 57, 57mm; QMW20793, 18°S 118°E, 250-390m, ♀, 53mm; NT C1006630, 8°38'S 132°E, 2♀, 39, 40mm; CSIRO, SS/1/91 #43, 27°S 112°E, ♀, 53mm.

DIAGNOSIS. Body, pereopods and other appendages with a fine pubescence. Adrostral carina ending just behind the first rostral tooth; postrostral carina low but reaching three-quarters the length of the carapace. A low gastro-orbital carina above a short, but distinct orbito-antennal sulcus. Branchiostegal spine on the border of the carapace and continuous with a prominent carina, which almost reaches the branchiocardiac carina; hepatic sulcus beside the posterior half of the branchiostegal carina. Branchiocardiac sulcus deep and almost reaching the posterior border of the carapace. A sub-distal, ventrolateral movable spine on the merus of pereopods 1-3. Carpus of pereopod 5 with 15-25 photophores, propodus with 16-22.

Colour. Red-orange, deeper on the margin of the carapace and rostrum, the posterior edges of the abdominal somites, the uropods and telson; pereopods lighter in colour.

REMARKS. This appears to be the commonest of the Australian species of *Aristeus* and is readily identifiable by the key characters.

DISTRIBUTION. Eastern Australia 10°-34°S, Arafura Sea 8°S 132°E, through Northwest Shelf to 29°S; 250-1050m. Known range: South Africa, Madagascar, Andaman Islands, Indonesia, South China, Philippines, Japan, Australia, New Caledonia, New Hebrides, Wallis and Futuna Islands, 250-1050m.

***Austropenaeus* Pérez Farfante
& Kensley, 1997**

Austropenaeus Pérez Farfante & Kensley, 1997: 4, figs 11, 12

DIAGNOSIS. Integument glabrous. Rostrum slender and upcurved, approx. 1.3-1.4 the length of the carapace in adult ♀♀, slightly shorter, but still exceeding the length of the carapace in adult ♂♂; with 3 dorsal teeth; adrostral carina short, starting at the base of the third tooth and ending behind the first tooth; postrostral carina reaching about one third of the carapace. Carapace with an antennal and a prominent branchiostegal spine on the margin of the carapace, with a short carina; hepatic sulcus wide and almost reaching the branchiocardiac sulcus; the latter barely defined, but almost reaching the posterior margin of the carapace; cervical sulcus short and indistinct; carapace otherwise almost featureless. Abdominal somite 3 without a distinct carina, but with a postero-dorsal spine; somites 4-6 each dorsally carinate and ending in a spine; telson acute with 4 pairs of lateral movable spines.

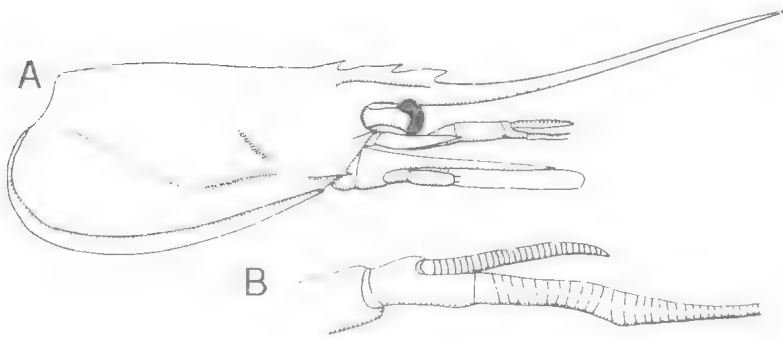


FIG. 5. A, *Austropenaeus nitidus* (Barnard, 1947) AMP55939, 33°51'S, 152°15'E, 1200m, ♀, 26mm. B, AMP55395, 34°53'S, 151°15'E, 1116m, ♂, 21mm, antennular flagella, lateral view.

Cornea slightly flattened, peduncle with a prominent mesial tubercle. Dorsal antennular flagellum flattened and reaching as far as the spine of the scaphocerite in females, slightly longer in males; ventral flagellum slender, terete and in the male with a proximal enlargement (Fig. 5B); scaphocerite not modified in the adult male, but with the dactyl of the third maxilliped thicker basally, with a finger-like distal part and shorter than in the female. Rudimentary exopods on all pereopods (Fig. 1), pereopods 1-3 slender and each with a sub-distal movable spine on the merus; the fourth and fifth more slender than the first to third. Dorsolateral lobule of petasma produced as a rounded process, well exceeding the ventromedian lobule; distal ventrolateral lobule semicircular and rounded; thelycum with apically pointed shield-shaped sternal plate on thoracic sternite 7, sternite 8 with low median prominence and paired anterolateral ridges.

REMARKS. This genus contains only *A. nitidus*, formerly included in *Plesiopenaeus*. The key characters enable *Austropenaeus* to be easily separated from *Plesiopenaeus*, notably by the almost featureless carapace. However, the rudimentary exopods on the pereopods, which separate it from other genera, are easily missed.

***Austropenaeus nitidus* (Barnard, 1947)**
(Figs 1, 5A,B)

Plesiopenaeus nitidus Barnard, 1947: 383, 1950: 622; Crosnier, 1978: 89; Kikuchi & Nemoto, 1986: 52.

MATERIAL. AMP39951, 33°40'S 152°E, 1115m, ♀, 30mm; AMP39979, 33°S 153°E, 1095m, 2♂, 21, 24mm, 5 ♀, 22-24mm; AM K24-20-03, E Sydney, 969-1006m, 5 ♀, 16-26mm; AMP55392, 38°S 150°21'E, 960m, ♀, 26mm; AMP 55395, 35°S 151°E, 1116m, 2♂, 21mm, 24mm, ♀, 26mm; AMP55396, 34°50'S 151°E, 1225m,

4 ♀, 25-33 mm; AMP55939, 33°51'S, 152°15'E, 1200m, ♀, 26mm; SAM (unregistered, Great Australian Bight approx. 34°S, 128 to 132°E, 927-1249m), 5 ♀, 30-37.5mm; CSIRO, SS/1/91 # 33, #47, #61, 29°35'S 111-113°E, 1101-1277m, ♂ 25 mm, 6 ♀, 25-31mm.

DIAGNOSIS. As for genus.

REMARKS. Kikuchi & Nemoto (1986) recorded 1 ♀ *A. nitidus* (as *Plesiopenaeus nitidus*) from the Northwest Pacific. It was collected around 22°N in a

0-5700m oblique tow, whereas all Southern Hemisphere *A. nitidus* have been collected in bottom trawls S of 26°S, nearly all between 1000-1300m. It is moderately common in the southern part of Australia, but to date it has not been found anywhere between 22°N and 26°S. Thus the identity of the Northwest Pacific species needs to be confirmed.

DISTRIBUTION. Australia S of 26°S, WA, through the Great Australian Bight and approaches to Bass Strait (approximately 40° S), to 27°S on the NSW coast, usual depth range 1000-1300m, where it appears to be moderately common (one recorded depth of 457m, may be an error). Known range: with the possible exception noted above *A. nitidus* appears to be an inhabitant of latitudes higher than 26° S; south Atlantic Ocean; off Cape of Good Hope and Natal, South Africa; Amsterdam and St. Paul Islands, south Indian Ocean; southern Australia, 457-1300m.

***Hemipenaeus* Bate, 1881**

Hemipenaeus Bate, 1881: 171, 186; 1888: 299; de Man, 1911: 23; Burkenroad, 1936: 90; Ramadan, 1938: 47; Anderson & Lindner, 1943: 300; Roberts & Pequegnat, 1970: 43; Crosnier, 1978: 74; Hayashi, 1983c: 366; Pérez Farfante & Kensley, 1997: 43.

Hemipenaeus Faxon, 1985: 198.

Aristeus (*Hemipenaeus*) Alcock, 1901: 31 [part].

Hemypenaeus Kikuchi & Nemoto, 1986: 52.

DIAGNOSIS. Integument glabrous. Rostrum usually short in both sexes, occasionally of moderate length in ♀♀; with 3 dorsal teeth; a short adrostral carina present; postrostral carina pronounced, reaching at least to the midlength of the carapace. Antennal and branchiostegal spines present, the latter on the margin of the carapace and with a prominent carina; cervical and

postcervical sulci present or absent; branchiocardiac carina and sulcus well-defined. Abdominal somite 3 with a prominent downcurved spine; somites 4-6 each with a dorsal carina; telson with 4 pairs of small movable spines in the posterior half, apex acute. Cornea moderately small, dorsoventrally flattened; ventral antennular flagellum not modified in the male. All pereopods with rudimentary exopods (Fig. 1); no movable meral spines on the pereopods. Petasma with distal margin of the dorsolateral lobule oblique and about the same length as the dorsomedian lobule; distal half of ventral costa free, the tip flattened with laterally directed projection. Thelycum with broad, anteriorly pointed plate on thoracic somite 7, somite 8 short and broad, roughly rectangular.

REMARKS. The genus contains only *H. carpenteri* and *H. spinidorsalis*. Both are deep water inhabitants, usually below 2000 m, which probably explains their apparent rarity. *H. carpenteri* is easily distinguished by its cervical and postcervical sulci (although these may be quite faint dorsally), which are totally lacking in *H. spinidorsalis*. Only *H. carpenteri* has been collected in Australian waters, although both species have a similar range.

***Hemipenaeus carpenteri* Wood-Mason, 1891**
(Fig. 6)

Hemipenaeus Carpenteri Wood-Mason, 1891: 189; Wood-Mason & Alcock, 1891b: 286; de Man, 1911: 6, 23.

Hemipenaeus triton Faxon, 1893: 215; 1895: 202, pl. 50, 1896: 163.

Aristeus (Hemipenaeus) carpenteri Alcock & McArdle, 1901: pl. 49, fig. 4.

Aristeus (Hemipenaeus) Carpenteri Alcock, 1901: 32.

Hemipenaeus carpenteri Burkenroad, 1936: 91; Ramadan, 1938: 48; Anderson & Lindner, 1945: 301; Roberts & Pequegnat, 1970: 43; Pequegnat & Roberts, 1971: 8, pl. 5D; Crosnier, 1978: 76, figs 27 c-d, 28 a-b, 29a, 1985: 862, 1994b: 369; Hayashi 1983c: 366, fig. 57.

MATERIAL. QMW13261, 16°54'S 147°E, 1473-1590m, ♀, 8mm; QMW13451, 17°S 148°E, 1500m, ♀, 35mm; TMH G4044, 21°S 113°E, 1139-1128m, ♀, 20mm; G4045, 23°S 113°E, 1460-1700, 2♂, 24, 24mm.

DIAGNOSIS. Rostrum short in both sexes, not exceeding the tip of the cornea in adults, slightly longer in the 8mm juvenile, with 3 dorsal teeth; a short adrostral carina present, ending between the first

and second rostral teeth; postrostral carina prominent, ending at 0.7-0.8 the length of the carapace. Gastro-orbital carina present, almost reaching the cervical sulcus. Antennal and branchiostegal spines present, the latter on the margin of the carapace and with a prominent carina reaching below the lower extremity of the cervical sulcus. A shallow hepatic sulcus, continuous with the deep branchiocardiac sulcus, which almost reaches the posterior margin of the carapace. Lower half of the cervical sulcus well-defined, with a very short carina at its lower end; upper part faint, but reaching the mid-dorsum; a faint postcervical sulcus present; submarginal carina sharp. Abdominal somite 3 with a large down-curved postero-dorsal spine; a dorsal carina on each of abdominal somites 4-6, that on the fourth weak. Ventral costa of the petasma free distally, the apex markedly flattened, with a laterally directed point. Thelycal plate on thoracic somite 7 with a long tapering anterior point.

Colour. Carapace deep blue, abdomen lighter blue anteriorly, changing to pinkish towards the telson; appendages pink to red.

REMARKS. The 20mm ♀ (Fig. 6) appeared to be close to sexual maturity, the thelycum being similar to that figured by Crosnier (1978, fig. 28a, b). The petasma of a mature ♂ does not appear to have been figured, but although one 24mm ♂ had well-developed petasmas halves they were not joined medially and it was therefore immature. Consequently, it has not been figured. The other ♂, although of identical size, was decidedly immature.

DISTRIBUTION. Western Australia, 20-22°S 113°E, 1100-1700m; NE Australia, 16-17°S 147°E; 1473-1590m. Known range: throughout the Indian Ocean, Indonesia, Japan, Australia, Wallis and Futuna Islands; Gulf of Panama and Galapagos Islands; W Atlantic, 900-3900m.

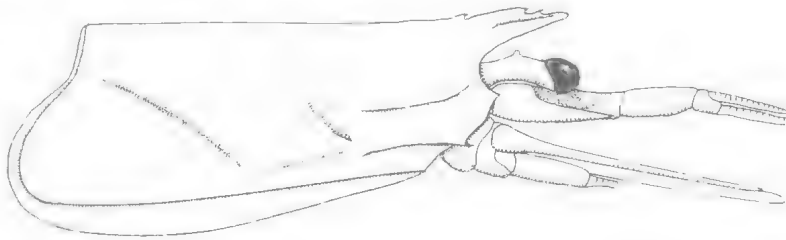


FIG. 6. *Hemipenaeus carpenteri* Wood Mason, 1891 TMHG4044, 20°55'S, 112°51'E, 1139m, ♀, 20mm.

Hepomadus Bate, 1881

Hepomadus Bate, 1881: 171, 189, 188: 319; Bouvier, 1908: 56; Milne Edwards & Bouvier, 1909: 194; Burkenroad, 1936: 86; Ramadan, 1938: 55; Pérez Farfante, 1973: 441; Crosnier, 1978: 47; Liu & Zhong, 1986: 28; Pérez Farfante & Kensley, 1997: 46.
Aristeus (*Hepomadus*) Alcock, 1901: 42.

DIAGNOSIS. Cuticle glabrous. Rostrum exceeding the antennular peduncle, with 3 dorsal teeth, including the epigastric. Postrostral carina variable; adrostral carina present. Antennal spine present; branchiostegal spine on the margin of the carapace at the end of a sharp carina; hepatic spine present, hepatic sulcus well-defined below the spine; branchiocardiac sulcus deep, the sulcus prominent and accompanying the carina almost to the margin of the carapace; cervical sulcus well defined and reaching to at least the dorsal region of the carapace. Abdominal somite 3 with or without a prominent posterodorsal spine; somites 4-6 dorsally carinate; telson with 4 pairs of lateral movable spines. Eye small, cornea flattened; ventral flagellum of antennule not sexually dimorphic; scaphocerite exceeding the antennular peduncle, its apex well exceeding the distolateral tooth. Pereopods with rudimentary exopods, sometimes lacking on the fifth; a distal movable spine on the merus of pereopods 1 & 2.

Dorsomedian lobule of the petasma nearly as long as the dorsolateral lobule, which is rounded distally; ventral costa with distal half free, the tip tapering. Thelycum with large elongate median protuberance on thoracic somite 7, with pointed anterior tip reaching the anterior rim of sternite 6.

REMARKS. This genus includes *H. glacialis* Bate, 1881, South Atlantic; *H. inermis* Bate, 1881, south-central Pacific Ocean; *H. tener* Smith, 1884, Atlantic, Indian and Pacific Oceans. All 3 species inhabit deep water, which may explain their apparent rarity. *H. inermis* appears to have been collected only once (type locality, depth 4665 m) and *H. glacialis* is almost as rare

(depth ca. 3400 m). However, *H. tener*, with a depth range of 765-5400m, mean 2400m, has been collected on a number of occasions, although still considered rare.

KEY TO THE SPECIES OF *HEPOMADUS*

1. A prominent posterodorsal spine on abdominal somite 3
 2
 No posterodorsal spine on abdominal somite 3
 *H. inermis*
2. Carapace with a pronounced hump behind the cervical sulcus, which interrupts the postrostral carina
 *H. glacialis*
 Carapace only slightly arched behind the cervical sulcus, postrostral carina continuing uninterrupted almost to the posterior margin of the carapace *H. tener*

***Hepomadus tener* Smith, 1884
(Fig. 7)**

Hepomadus tener Smith, 1884: 409, pl. 9, fig. 7-8; 1887; Bouvier, 1908: 57, pl. 1, fig. 5, pl. 13, figs 1-12; Burkenroad, 1936: 86; Ramadan, 1938: 55; Roberts & Pequegnat, 1970: 43, fig. 3; Pequegnat & Roberts, 1971: 9; Pérez Farfante, 1973: 442, figs 1-8; Crosnier, 1985: 860, 1994b: 369; Liu & Zhong, 1986: 28, fig. 10.
Hepomadus tener? Wood-Mason & Alcock, 1981: 189.
Aristaeus (*Hepomadus*) *tener*? Alcock, 1901: 42.
Hepomadus glacialis Milne Edwards & Bouvier, 1909: 194, figs 13-19, pl. 1 fig 3.

MATERIAL. TMH G4046, 22°S 113°E, 1460-1700m, 4♂, 21-34mm, 2♀, 29, 37mm.

DIAGNOSIS. Cuticle flexible and glabrous. Rostrum styliform, upturned, its length relative to that of the carapace increasing with size, being shorter in smaller specimens and longer in larger specimens; with 3 dorsal teeth including the epigastric; adrostral carina well defined, reaching at least the base of the epigastric tooth. Postrostral carina almost reaching the posterior margin of the carapace, the postrostral region of the carapace slightly convex. Antennal, hepatic and branchiostegal spines present, the latter on the margin of the carapace at the end of a prominent carina, which extends as far as the hepatic spine. An orbito-antennal sulcus present, continuous

with a deep hepatic sulcus, which meets the branchiocardiac sulcus, before turning ventrad. Branchiocardiac sulcus deep, the carina prominent, both almost reaching the posterior margin of the carapace, before turning ventrad. Cervical sulcus well-defined and reaching the postrostral carina; postcervical sulcus faint.

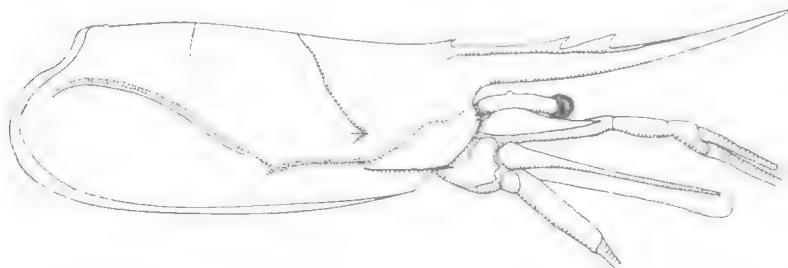


FIG. 7. *Hepomadus tener* Smith, 1884, TMH4046, 22°S, 113°8'E, 1460-1700m (aborted trawl), ♂, 31mm.

Abdominal somite 3 with weak dorsal carina on its posterior half ending in a large, down-curving spine; somites 4-6 each with a sharp dorsal carina; telson with 4 small movable spines. Optic peduncle long, cornea small and slightly flattened. Scaphocerite exceeding the antennular peduncle, the tip longer than the distolateral spine. Pereopods 1 & 2 each with a prominent movable meral spine. Dorsomedian lobules of petasma diverging distally; dorsolateral lobule rounded distally, about as long as the dorso-median lobule; ventral costa prominent, the distal half free and ending in bluntly pointed tip, directed laterally. Thelycum with an elongate plate on thoracic sternite 7, the sides rounded and pointed apex reaching almost to sternite 5; sternite 8 subrectangular, more or less convex.

REMARKS. Pérez Farfante (1973) found a good deal of variation in specimens from the Atlantic, but nevertheless *H. tener* is a distinctive species.

DISTRIBUTION. NW Australia, 22°S 113°E; 1460-1700m. Known range: Zanzibar, Madagascar, Réunion, central Indian Ocean, Bay of Bengal, Australia, Wallis and Futuna Islands, W and E Atlantic Ocean, 765-5400m.

Parahepomadus Crosnier, 1978

Parahepomadus Crosnier, 1978: 47; Liu & Zhong, 1986: 30; Pérez Farfante & Kensley, 1997: 48.

TYPE SPECIES. *Parahepomadus vaubani* Crosnier, 1978 (monotypic).

DIAGNOSIS. Cuticle thin and flexible, finely pubescent. Rostrum often short in adults of both sexes, not reaching beyond the second segment of the antennular peduncle, but may be slender and well exceeding the peduncle. Adrostral carina reaching just past the first rostral tooth; postrostral carina reaching about half the carapace. Postorbital spine present, continuous with the gastro-orbital carina, which almost reaches the shallow cervical sulcus, the latter limited to the lateral region of the carapace. A very small antennal spine may be present, absent in the larger specimens, but with the low antennal carina ending in a minute

tubercle just behind the carapace margin; orbito-antennal sulcus deep, continuous with the hepatic and branchiocardiac sulci. A large branchiostegal spine on the margin of the carapace, the branchiostegal carina reaching the branchiocardiac carina; the latter almost reaching the posterior margin of the carapace. Eye dorsoventrally flattened, with a small median tubercle on the peduncle; lower antennular flagellum with a slight sigmoidal flexure in males. Scaphocerite very wide; exopods usually absent from pereopods; minute subdistal meral spines on pereopods 1 & 2. Petasma very wide with rounded median lobe; thelycum a large concave setose plate, with prominent anterior point, on thoracic somite 7. Uniformly orange.

Parahepomadus vaubani Crosnier, 1978 (Fig. 8A, B)

Parahepomadus vaubani Crosnier, 1978: 48, figs 20-22, 1989, 1994a; Liu & Zhong 1986: 30, fig. 11.

MATERIAL. NT Cr007084, 13°S 122°E, 900-1000m, ♂, 48mm, ♀, 67mm; NTCr007085, 13°06' 122°18'E, 900-1000m, ♂, 53, 54mm, 2♀, 57, 58mm.

DIAGNOSIS. As for genus.

REMARKS. Two specimens had rudimentary exopods on pereopods 1-5, which could confuse identification, but the postantennal spine sets this apart from other members of the family. The normal very long slender rostrum is apparently subject to breakage, since most adults have a shortened rostrum (Crosnier, 1978, fig. 20).

DISTRIBUTION. Off the Northwest Shelf of Australia, 13°S 122°E; 900-1000m. Known

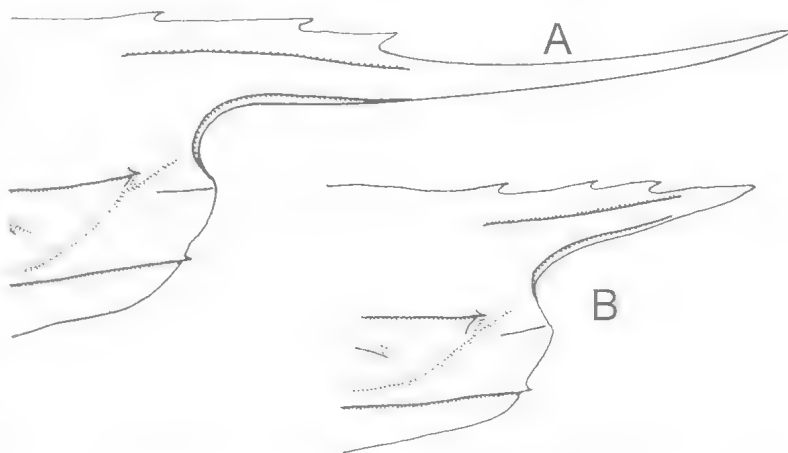


FIG. 8. *Parahepomadus vaubani* Crosnier, 1978 NT CR007085, 13°6'S 122°18'E, 900-1000m. A, ♀, 58 mm, rostrum. B, ♂, 54mm, short rostrum.

range: Madagascar, Indonesia, Australia, Philippines, 750-1525m.

Plesiopenaeus Bate, 1881

Aristeus Bate, 1881: 187 [part]; 1888: 309 [part].

Aristaeus Wood-Mason 1891: 278 [part].

Plesiopenaeus Bate, 1881: 188; Bouvier, 1908: 63 [part]; Burkenroad, 1936: 94; Ramadan, 1938: 49 [part]; Barnard, 1950: 621; Crosnier, 1978: 85; de Freitas, 1985: 20; Pérez Farfante & Kensley, 1997: 50.

Plesiopenaeus Faxon, 1895: 199.

Aristeopsis Bouvier, 1908: 61; Milne Edwards & Bouvier, 1909, 197.

DIAGNOSIS. Integument firm, glabrous. Rostrum longer than the carapace in juveniles and adult ♀♀, shorter in ♂♂; with 3 dorsal teeth. Antennal and branchiostegal spines prominent, the latter on the margin of the carapace and continuous with a sharp carina; orbital, postantennal, pterygostomial and hepatic spines absent; gastro-orbital carina present; cervical sulcus variable; branchiocardiac carina well-defined. Posterior half of abdominal somite 3 and 4-6 dorsally carinate. Telson with 4 pairs of movable lateral spines, apex acute. Cornea slightly flattened; a strong tubercle at about midlength of the peduncle. Dorsal antennular flagellum flattened, ventral flagellum elongate, slender and not modified in the adult ♂. Scaphocerite with thickened margin ending in a short spine at about 0.8 the length of the lamella. Merus of pereopod 1 or 1 & 2 with a sub-distal movable spine; exopods on all thoracic appendages, those of the pereopods rudimentary. Ventral costa of petasma free distally, the apical part hooked with tip directed laterally; thelycum with sternum of thoracic somite raised and shield-like, with acute apex.

REMARKS. This genus contains *P. armatus* and *P. coruscans*, *P. edwardsianus* and *P. nitidus* having been transferred to the monotypic genera *Aristaeopsis* and *Austropeneus*, respectively (Pérez Farfante & Kensley, 1997). *P. armatus* is readily distinguished by a prominent dorsal spine

on abdominal somite 3, whereas *P. coruscans* has none.

Plesiopenaeus armatus (Bate, 1881)

(Fig. 9)

Aristeus armatus Bate, 1881: 188, 1888: 312, pls. 45, 46.

Aristeus tridens Smith 1884: 104, pl. 9, 1886b: 189, 192, 193, 1887: 689, pl. 19.

Aristaeopsis armata Wood-Mason & Alcock, 1891b: 285.

Plesiopenaeus armatus, Faxon, 1895: 199, 1896: 163; Burkenroad, 1936: 95; Ramadan, 1938: 51, Anderson & Lindner, 1945: 301; Roberts & Pequegnat, 1970: 46; Pequegnat & Roberts, 1971: 8, pl. 5; Wasmer, 1972: 259; Crosnier & Forest, 1973: 294, fig. c-d; Crosnier, 1978: 93, fig. 33b, 1985: 863, 1994b: 369; Hayashi, 1983c: 368, fig. 58a-d; Pérez Farfante & Kensley, 1997: fig. 19.

Aristaeus (Aristaeopsis) armatus Alcock, 1901: 41.

Aristeopsis armatus Bouvier, 1905: 983; de Man, 1911: 6, Balss, 1925: 222.

Aristeopsis armatus var. *tridens* Bouvier, 1908: 62, pl. 11, fig. 6; Milne Edwards & Bouvier, 1909: 197, figs 4-7, 20-27; de Man, 1911: 6; Bouvier, 1922: 12.

Plesiopenaeus armatus tridens Burkenroad, 1936.

MATERIAL. AMP39932, 20°42'S 160°E, 2450m, ♂, 57mm, ♀, 56mm; AMP39939, 12°S 146°E, 2053m, ♀, 35mm; QMW13666 14°27'S 146°34'E, 1930-1942m, 4 ♀, 47-57mm; QMW136667, 13°40'S 147°43'E, 2884-2932m, ♂, 63mm, ♀, 54mm; QMW13668, 13°29'S 147°13'E, 2490-2542m, ♂, 60mm, 3 ♀, 55, 70, 80mm; QMW13669 13°40'S 146°57'E, 1880-1921m, 3 ♂, 57, 61, 65mm, ♀, 43mm.

DIAGNOSIS. Carapace glabrous. Rostrum long, well exceeding the scaphocerite, with 3 dorsal teeth; adrostral carina ending in front of the first tooth; postrostral carina low and reaching about half the carapace. Antennal spine with a short carina; branchiostegal spine prominent, on the margin of the carapace and with a carina extending past the beginning of the branchiocardiac carina; the latter reaching the posterior margin of the carapace, both carina and sulcus well defined; orbito-antennal sulcus deep and continuous with the wide hepatic sulcus which becomes indistinct at the level of the branchiocardiac carina. A low gastro-orbital carina present; cervical carina and sulcus present in the lateral region of the carapace only, the latter

very wide and shallow. Abdominal somite 3 without a distinct dorsal carina, somites 4-6 each with a carina; somites 3-6 each ending in a large tooth, that of somite 6 smaller; pleura of somites 3-5 postero-ventrally mucronate. Eye small, flattened; stylocerite

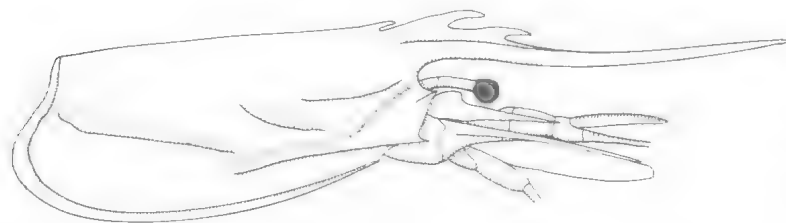


FIG. 9. *Plesiopenaeus armatus* (Bate, 1881) AMP39939, 11°42'S, 145°37'E, 2053m, ♀, 39mm.

exceeding the second antennular segment; scaphocerite not sexually dimorphic; exopods on pereopods rudimentary, without setae; a subdistal spine on the merus of pereopods 1 & 2. Thelycal plates on thoracic somite 5-8 with a prominent median ridge.

Colour. Uniformly wine red.

REMARKS. This is one of the largest aristeids, the 80 mm ♀ being in the upper size range. *Aristaeopsis edwardsiana* reaches a comparable size.

DISTRIBUTION. NE Australia 11-21°S, Lord Howe Rise 27-30°S 159°40'E; 1880-2930m. Cosmopolitan, W and E Atlantic, Indo-Pacific from Madagascar and Zanzibar, Bay of Bengal, Australia, Philippines, off Japan, off Hawaiian and Tuamotu Islands, W coast USA, 752-5413m.

Plesiopenaeus coruscans

(Wood-Mason, 1891)

Aristeus coruscans Wood-Mason in Wood-Mason & Alcock, 1891b: 280, fig. 6.

Aristaeus coruscans Wood-Mason, 1892: pl. 2, fig. 3; Faxon, 1895: 198.

Aristaeus (Plesiopenaeus) coruscans Alcock, 1901: 37.

Plesiopenaeus coruscans Bouvier, 1908: 69; de Man, 1911: 6; Burkenroad, 1936: 95, fig. 61; Roberts & Pequegnat, 1971: 46; Crosnier, 1978: 94, fig. 33c-f; Liu & Zhong 1986: 47, fig. 19.

MATERIAL. NTCR006994, 13°S 122°E, 900-1000m, ♀, 63mm.

DIAGNOSIS. Rostrum exceeding the antennular peduncle in juveniles and adult ♀♀, shorter in adult ♂♂; with 3 dorsal teeth; adrostral carina extending past first rostral tooth; postrostral carina nearly reaching the posterior margin of the carapace. Antennal spine with a carina almost reaching the orbito-antennal sulcus; gastro-orbital carina prominent and reaching the cervical sulcus; branchiostegal spine large and on the margin of the carapace, with prominent carina reaching the branchiocardiac carina. Hepatic sulcus continuous with the branchiocardiac sulcus, which, with the carina almost reaches the posterior margin of the carapace; cervical sulcus shallow, but almost reaching the mid-dorsum; a short carina on the lower part. A dorsal carina on the posterior half of abdominal somite 4 and on the full length of somite 5 & 6. Posteroventral pleura of abdominal somites 3-5 not mucronate. Eye dorsoventrally flattened, the peduncle long and with a prominent mesial tubercle. Pereopod 1 only with a sub-distal spine on the merus; rudimentary exopods on all pereopods. Thelycum with prominent anteriorly pointed flat

sternal plate on thoracic somite 7; somite 8 with a transverse low triangular projection.

Colour. Clear orange.

REMARKS. The sole specimen available was badly damaged and unsuitable for illustration (Crosnier, 1978). Its integument was exceptionally thin and flexible, more so than most other members of this family, and it could have been newly moulted. It is a large species and so far rare (Crosnier, 1978 noted that there were only 4 specimens known besides the 2 from Madagascar). Other features which distinguish it from *P. armatus* besides the absence of a large dorsal abdominal spine, are the cervical sulcus which almost reaches the mid-dorsum, lack of a spine on the merus of pereopod 2, lack of any armature on the pleura of the abdomen and a median carina on the thelycum.

DISTRIBUTION. Northwest Shelf of Australia, 900-1000m. Known range: Indian Ocean from Madagascar, the Arabian Sea, Bay of Bengal to NW Australia and the Atlantic Ocean, near the Bahamas, 900-2367m.

***Pseudaristeus* Crosnier, 1978**

Hemipenaeus Bate, 1881: 186 [part]; Ramadan, 1938: 47 [part].

Aristaeus Wood-Mason, 1891: 278 [part].

Aristaeus (Hemipenaeus), Alcock, 1901: 31 [part].

Pseudaristeus Crosnier, 1978: 81; de Freitas, 1985: 11; Pérez Farfante, 1987: 312; Pérez Farfante & Kensley, 1997: 52.

DIAGNOSIS. Integument pubescent. Rostrum elongate, when undamaged reaching well beyond the scaphocerite; with 3 dorsal teeth; postrostral carina defined. Carapace with antennal and marginal branchiostegal spines, the latter continuous with a strong carina; hepatic sulcus present; orbital, pterygostomial and hepatic spines absent; cervical sulcus reaching the mid-dorsum, a postcervical sulcus present; branchiocardiac carina and sulcus well defined. Abdominal somites 1-3 dorsally rounded, somites 4-6 dorsally carinate, somite 4 carinate in its posterior half only. Telson with slender acute apex, with 4 pairs of movable lateral spines. Eye well developed, dorsoventrally flattened; peduncle with a small tubercle on the mesial margin. Scaphocerite not sexually dimorphic. Pereopods without exopods, 1 & 2 each with a subdistal movable spine on the merus. Pereopod 3 without a podobranch. Petasma with distal margin of dorsolateral lobule oblique, reaching or slightly surpassing the median lobe; ventral costa distally free for ca. half its length, turning mesially. Thelycum open, with large lanceolate

plate on thoracic sternite 7; a broad plate on sternite 8, produced into anterolateral hoods.

The genus includes *P. crassipes* (Wood-Mason, 1891), *P. gracilis* (Bate, 1888), *P. kathleenae* Pérez Farfante, 1987, *P. protensus* Pérez Farfante, 1987, *P. sibogae* (De Man, 1911), and *P. speciosus* (Bate, 1881). The last is an Atlantic species and *P. gracilis* is known only from the Philippines. *P. sibogae* and *P. kathleenae* have both been collected from Australian seas, while *P. crassipes* has been found in Indonesia and could also be an Australian species. Pérez Farfante (1987) erected *P. protensus* on the differences in proportions of the thelycal plates, based on 2 ♀♀ from Indian seas, but Crosnier (1994a) considered it a doubtful species. More specimens, particularly a mature ♂ will be necessary to validate *P. protensus*.

KEY TO THE INDO-WEST PACIFIC SPECIES OF *PSEUDARISTEUS*

1. Pereopods covered with minute setae. Optic peduncle long, mesial margin at least 1.4 the width of the distal extremity *P. sibogae*
Pereopods not covered with setae. Optic peduncle relatively short, mesial margin 1.3 or less the width of the distal extremity 2
2. Third segment of antennular peduncle expanded laterally, forming a prominent subtriangular projection in males and a smaller rounded structure in females *P. kathleenae*
Third segment of antennular peduncle not expanded laterally 3
3. Males with ventral antennular flagellum sinuous proximally, with a narrow band of small dense setae, distal to the tip of the dorsal flagellum. Median thelycal plate of thoracic somite 7 expanded in a pair of posterolateral prominences *P. gracilis*
Males with ventral antennular flagellum straight proximally and without a band of small setae. Median thelycal plate of thoracic somite 7 without posterolateral prominences *P. crassipes*

Pseudaristeus kathleenae Pérez Farfante, 1987 (Fig. 10A,B)

- Aristaeus crassipes* Wood-Mason, 1891 [part]; Alcock, 1901a [part].
Hemipenaeus crassipes De Man, 1911: 24 [part]; 1913: pl. 2, fig. 4a-c; Kemp & Seymour Sewell, 1912: 17, pl. 1, fig. 8 [part]; Balss, 1925 [part].
Pseudaristeus kathleenae Pérez Farfante, 1987: 314, figs 1-9; Crosnier, 1994a: 353; Pérez Farfante & Kensley, 1997: figs 21-23.

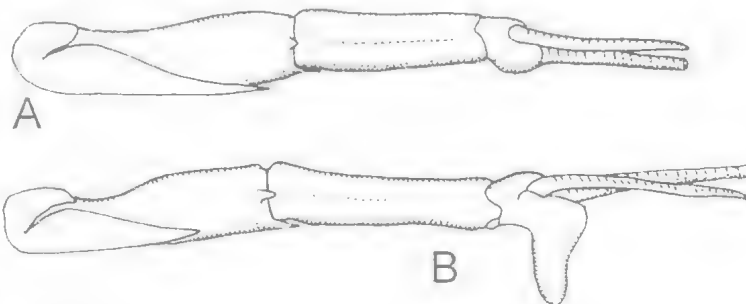


FIG. 10. *Pseudaristeus kathleenae* Pérez Farfante, 1987. A, NT CR 006629, 9°17'S 131°8'E, 297m, ♀, 36.5mm, antennule. B, ♂, 23.5mm, antennule (after Pérez Farfante, 1987, fig. 2).

MATERIAL. NT Cr006629, 9°17'S 131°E, 297m, 3 ♀, 29, 31, 36mm (all damaged and unsuitable for illustration).

DIAGNOSIS. Carapace finely pubescent, cuticle thin. Rostrum usually exceeding the antennular peduncle in ♀♀ and immature ♂♂, much shorter in mature ♂♂; with 3 dorsal teeth; adrostral carina ending just behind the first rostral tooth; postrostral carina distinct up to the cervical sulcus, becoming indistinct thereafter and reaching about 0.75 the carapace. Antennal spine prominent with the carina reaching the shallow orbito-antennal sulcus; gastro-orbital carina well defined and reaching the cervical sulcus. Branchiostegal spine large, on the margin of the carapace and continuous with a prominent carina, which almost reaches the branchiocardiac carina. Hepatic sulcus continuous with the orbito-antennal sulcus and turning sharply downwards at its junction with the branchiocardiac sulcus. Branchiocardiac carina forming a wide arc, which runs downward into the posterior margin of the carapace. Cervical sulcus shallow, but crossing the mid-dorsum, the carina limited to a short prominent shallow arc in its ventral region; postcervical sulcus not quite reaching the mid-dorsum and curving anteriorly towards the cervical sulcus, but not meeting it; with a low carina in its ventral region. Abdomen dorsally carinate on somites 4-6, each carina ending in a tooth. Mesial length of the optic peduncle/ maximum width at the cornea about 1.0. Tip of stylocerite well short of the disto-lateral spine of the first segment of the antennular peduncle; third segment with a large triangular ventro-lateral expansion ♂ and a rounded bulbous swelling in ♀ (Fig. 10A, B). Third maxilliped dimorphic, in the male the dactyl inserted subapically in the propodus, curved and of uniform width, with a dense tuft of

subapical setae. Pereopods 1 & 2 with subdistal spine on the merus. Dorsolateral lobule of petasma expanding distolaterally before tapering to a bluntly pointed mesial apex. Sternal plate of thoracic somite 7 a large densely setose lanceolate plate, maximum width about 0.65 the length, plate on somite 8 produced anteriolaterally into a pair of short hoods.

REMARKS. Although the genus has been revised (Pérez Farfante, 1987) *P. sibogae*, *P. kathleenae* and *P. crassipes* have similar ranges and may still be confused. *P. sibogae* is reasonably distinctive (see under *P. sibogae* for a discussion of these features), but the ♀♀ of *P. kathleenae* and *P. crassipes* are difficult to distinguish. The ♂ *P. kathleenae* is readily separated from *P. crassipes* by the sexually dimorphic antennule and third maxilliped and the expanded dorsolateral lobule of the petasma. In contrast, in the ♀ only the swollen third segment of the antennular peduncle of *P. kathleenae* clearly distinguishes it from *P. crassipes* and this feature is easily missed. The thelycal plate on thoracic somite 7 appears to be relatively broader in *P. kathleenae* (width/length 0.67-0.75 versus 0.43-0.55 in *P. crassipes*). Otherwise the thelyca are similar. Crosnier (1978) showed that pereopods 1 & 2 were stouter in *P. sibogae* than in *P. crassipes* and *P. gracilis* by comparing the ratios of length/width of the carpi. These ratios for pereopods 1 & 2 are 8.5-8.9 and 10.5 respectively in *P. kathleenae* and 8.6-9.3 and 10.1-12.9 in *P. crassipes*, and so these 2 species are indistinguishable by this means. Thus the relative broadness of the thelycal plate is the only feature to assist identification of ♀♀ when the presence or absence of the swelling of the third segment of the antennular peduncle is in doubt.

DISTRIBUTION. Australia, Arafura Sea 9°S 131°E, 297m. Known range: Southern India, Indonesia, Arafura Sea, Philippines, 297-1225m. (The Australian location is much shallower than the other records of depth, which start at 549m.)

***Pseudaristeus sibogae* (de Man, 1911)
(Fig. 11A-E)**

Hemipendaeus sibogae de Man, 1911: 25, 1913, pl. 2, fig. 5, 5a-c; Ramadan, 1938: 48; Anderson & Lindner, 1945: 301.

Pseudaristeus sibogae Crosnier, 1978: 83, figs 27a, 30a-c, 1994a: 353; de Freitas, 1985: 12, fig. 11-5; Pérez Farfante, 1987: 332, fig. 18.

MATERIAL. AMP41894, 22°S 114°E, 1158m, ♀, 37mm; AMP55940, 20°S 113°E, 914m, ♂, 24mm, ♀, 36mm; CSIRO SS1091, #13, #22, #24, #49, 23-28°S 111-114°E, 854-1305m, 3♂, 31, 32, 33mm, 10♀, 31-43 mm; QM W24354, 33°58'S 131°22'E, 1000m, ♂, 33mm.

DIAGNOSIS. Body finely pubescent. Rostrum normally exceeding the antennular peduncle in both sexes; with 3 dorsal teeth; adrostral carina ending at the first rostral tooth; postrostral carina reaching about 0.9 the length of the carapace. Antennal spine with carina; gastro-orbital carina and orbito-antennal sulcus present. A prominent branchiostegal spine on the margin of the carapace, with sharp carina reaching the branchiocardiac carina; hepatic sulcus wide; branchiocardiac carina low, but well-defined, the carina and sulcus reaching the posterior margin of the carapace, where they turn down, the sulcus joining the submarginal sulcus. Cervical sulcus shallow, but crossing the mid-dorsum, the carina limited to a short prominent shallow arc in its ventral region; a postcervical sulcus present, not

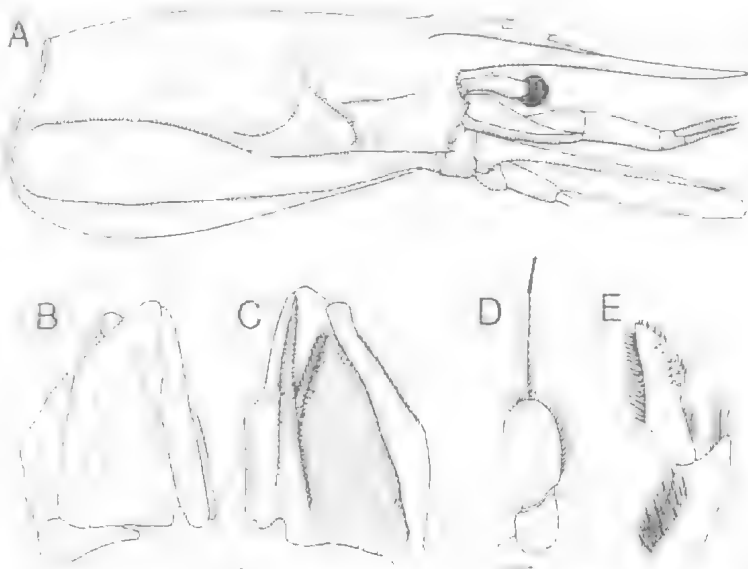


FIG. 11. A, *Pseudaristeus sibogae* (de Man, 1911) QMW25354, 33°58'S, 131°22'E, 1000m, ♂, 33mm; B, dorsal aspect of petasma; C, ventral aspect of petasma; D, appendix masculina; E, propodus and dactyl of maxilliped 3. (Scalebar = 1mm).

quite meeting the mid-dorsum; a short auxiliary posthepatic carina and sulcus running in an arc from the cervical sulcus towards the branchiocardiac sulcus. A dorsal carina beginning at the middle of abdominal somite 3, somites 3-6 each ending in a small tooth. Cornea flattened, the mesial length of the peduncle at least 1.4 times the maximum distal width at the cornea. Third maxilliped sexually dimorphic (Fig. 11 E); pereopods 1-3 relatively robust, 4 & 5 much more slender, all covered with a fine pubescence. Distal half of dorsomedian lobule of petasma free and reaching almost as far as the distolateral lobule (Fig. 11 B, C); the latter tapering towards the midline, apex rounded; ventral costa prominent, the distal half free, with truncated tip; ventral surface covered with fine setae. Appendix masculina with ovate outer plate; inner plate (appendix interna) about 2.5 times the length of the outer plate, flexible and tapering (Fig. 11D). Thelycal plate on thoracic somite 8 produced anterolaterally into short hoods, that on somite 7 lanceolate, broad (width 0.6 length), without posterolateral prominences.

Colour. Orange.

REMARKS. *P. sibogae* has 4 distinctive features, which while reliable, are not completely definitive: the pubescent pereopods; the relatively long optic peduncle; the well-defined auxiliary carina and sulcus above the posterior hepatic sulcus; the stouter pereopods. The ratio of length/width of the optic peduncle was only 1.45 in these specimens, although Pérez Farfante (1987) recorded 1.5-1.75 (but such measurements are subject to operator variability). Other species also have at least indications of an auxiliary sulcus. Crosnier (1978) showed that the pereopods were stouter than in other species by comparing the ratios of length/width of podomeres of the pereopods, the ratios of the first and second in particular being appreciably smaller in *P. sibogae* than in other species. In the above specimens examined, the ratios of length/width of the carpus of pereopods 1 & 2 were 5.8-6.7 and 7.0-7.2, respectively,

which are close to those of Crosnier. Thus the only dubious feature in the specimens examined was the length/width ratio of the optic peduncle, but this appears to be a variable characteristic. Pérez Farfante (1987) used features of the genitalia to define species, but again ratios of length/breadth of thelycal plates appear to be variable.

The petasma of a mature ♂ (QM W24354, Fig. 11B, C), previously undescribed, is similar to that of *P. crassipes*, except for the fine setae on the ventral surface.

DISTRIBUTION. Western Australia 20-28°S, Great Australian Bight; 854 -1305m. Known range: Off Natal, South Africa, Madagascar, Indonesia, Australia, 834-1305m.

Family BENTHESICYMIDAE Wood-Mason, 1891

Benthescymina Wood-Mason, 1891: 286.
Benthescymae Bouvier, 1908: 16; Burkenroad, 1936: 15; Anderson & Lindner, 1943: 290; Balss, 1957: 1517; Firmizi, 1960: 321; Roberts & Pequegnat, 1970: 32.
Benthescyminae Crosnier, 1978: 14; Hayashi, 1983d: 438.
Benthescymidae Pérez Farfante & Kensley, 1987: 56.

DIAGNOSIS. Integument thin and soft. Rostrum truncate and blade-like, with the tip usually falling short of the cornea, occasionally not reaching much beyond it; without adrostral carina; dorsally armed only with not more than 3, usually 2 or fewer dorsal teeth. Branchiostegite with a more or less deep antero-ventral emargination, with branchiostegal spine either on or just behind the carapace margin. Hepatic spine present or absent; hepatic carina and sulcus usually well defined; cervical and usually the postcervical sulcus reaching the dorsal mid-line. Telson with 1-4 pairs of movable lateral spines, apex usually acute, sometimes truncate. Eye medium to small, the peduncle with a mesial tubercle; prosartema usually only a tuft of setae; both antennular flagella long and filiform. Exopods on all maxillipeds, present or absent on pereopods. Petasma open, usually broadly lamellar, with the flexible part of the ventrolateral lobule attached to the dorsolateral lobule for most

TABLE 3. Distribution of branchiae and epipods on the thoracic somites of the genera of the Benthescymidae.

Genus	Pleurobranchs Somites 3-8	Arthrobranchs Somite 1	2 Arthrobranchs Somites 2-7	Podobranchs Somites 2-6	Epipods Somites 1-7
<i>Bentheogennema</i>	+	l	+	+	+
<i>Benthescymus</i>	+	s	+	+	+
<i>Benthonetes</i>	+	l	+	2-5. 6s	+
<i>Gennadus</i>	+	r	+	somite 2 only	+

or all of its length; ventral costa entirely attached. Thelycum open or closed with seminal receptacles formed by paired sternal invaginations at the base of pereopods 3. Arrangement of branchiae and epipods in the genera of the Benthescymidae is shown in Table 3.

KEY TO THE GENERA OF THE BENTHESICYMIDAE

1. Podobranchs on thoracic somites 2-6; telson usually armed with more than one pair of lateral movable spines . . . 2
Podobranchs present on thoracic somite 2 only; telson armed with only one pair of lateral movable spines . . . *Gennadas*
2. Telson apically pointed. At least two abdominal somites dorsally carinate. 3
Telson apically truncate; only abdominal somite 6 dorsally carinate *Bentheogennema*
3. Dactyls of pereopods 4 & 5 not multiarticulate and not markedly elongate; usually a dorsal carina on abdominal somite 4, as well as 5 & 6; dactyl of maxilliped 3 spinous and setose. *Benthescymus*
Dactyls of pereopods 4 & 5 multiarticulate and markedly elongate; a dorsal carina on abdominal somites 5 & 6 only; dactyl of maxilliped setose but not spinous *Benthonectes*

Gennadas is well represented in Australian seas by 8 species, but so far only 2 *Benthescymus* species have been positively identified, with a possible third new species; *Bentheogennema* has yet to be recorded. NTCR007066 was identified as *Benthonectes filipes* by Dr A. Crosnier in 1990. However, I found that it is now too badly damaged to be positively identified, is of no value as a reference specimen, and a description of this species has therefore not been included (Pérez Farfante & Kensley, 1997 for description and figures).

Benthescymus Bate, 1881

Benthescymus Bate, 1881: 171, 190, 1888: 326; Alcock, 1901: 42; de Man, 1911:13; Burkenroad, 1936: 23; Anderson & Lindner, 1943: 296; Tirmizi, 1960: 322; Crosnier, 1978: 15; Hayashi, 1983d: 438; Squires, 1990: 21; Kikuchi & Nemoto, 1991: 64; Pérez Farfante & Kensley, 1997: 59.

Benthonectes Smith, 1884: 391.

Gennadas Alcock, 1901: 46 [part].

DIAGNOSIS. Rostrum apically acute, often falling short of the cornea, with 0-3 dorsal teeth. Branchiostegal spine on or just behind the margin of the carapace, continuous with hepatic carina; hepatic spine present or absent; cervical, postcervical, hepatic and branchiocardiac sulci well marked. Abdominal somites 5 & 6 dorsally carinate, usually a low carina on the posterior half of the fourth. Telson with 4 pairs of movable lateral spines, apex acute. Eye medium to small,

the cornea slightly wider than the peduncle, brown to black-pigmented; a conical mesial process at about half the length of the peduncle. Dactyli of pereopods 4 & 5 slender and uniarticulate. Petasma with dorsolateral lobule broad, sometimes distally bilobed, longer than the ventrolateral lobule.

KEY TO THE INDO-WEST PACIFIC SPECIES OF *BENTHESICYMUS*

1. Branchiostegal spine at margin of carapace, branchiostegal carina not sharp; dactylus of 3rd maxilliped triangular, with only one strong spine at the tip (Group 1) 2
Branchiostegal spine just behind margin of carapace, branchiostegal carina very sharp; dactylus of 3rd maxilliped subrectangular, distal margin with more than one strong spine (Group 2) 11
2. Posterolateral margin of abdominal somite 4 crenate. . 3
Posterolateral margin of abdominal somite 4 not crenate 4
3. Hepatic spine present; posterolateral margin of abdominal somite 5 without a spine; merus and ischium of maxilliped 3 each with a small acute spine on the median distal part. *B. crenatus*
Hepatic spine absent; posterolateral margin of abdominal somite 5 with a small spine; merus and ischium of maxilliped 3 each without spines on the median distal part *B. laciniatus*
4. Hepatic spine present. 5
Hepatic spine absent 10
5. Abdominal somite 3 with a postero-dorsal spine *B. brasiliensis*
Abdominal somite 3 without a postero-dorsal spine . . 6
6. Abdominal somite 4 with a postero-dorsal spine **B. urinator*
Abdominal somite 4 without a postero-dorsal spine . . 7
7. Merus of 2nd maxilliped more than 3.5 times as long as broad. *B. strabus*
Merus of 2nd maxilliped less than 3 times as long as broad. 8
8. Abdominal somites 5 & 6 each with a postero-dorsal spine 9
Abdominal somites 5 & 6 each without a postero-dorsal spine. *B. iridescens*
9. Posterior rostral tooth usually anterior to the level of the orbital margin. *B. longipes*
Posterior rostral tooth well behind the level of the orbital margin **B. seymouri*
10. Abdominal somite 6 more than 2.5 times as long as the fifth somite *B. brevirostris*
Abdominal somite 6 less than 2.5 times as long as the fifth somite *B. carinatus*
11. Hepatic spine present *B. tanneri*
Hepatic spine absent 12
12. Abdominal somite 5 with a long spine extending backwards 13
Abdominal somite 5 without a long postero-dorsal spine 14
13. Long spine of abdominal somite 5 extending backwards from the middle of the dorsal mesial margin . *B. bartletti*

- Long spine of abdominal somite 5 extending backwards from the postero-dorsal margin. *B. tirmiziae*
 14. Postero-dorsal tip of abdominal somite 6 curving upwards *B. alius*
 Postero-dorsal tip of abdominal somite 6 directed horizontally *B. investigatoris*

*See discussion under *B. urinator howensis* sp. nov.

Only *B. investigatoris*, *B. urinator* and a possible new species have been collected from Australian seas, but probably more species are present as Kikuchi & Nemoto (1991) recorded 8 species from the NW Pacific and Crosnier (1978, 1985) 8 from the W Indian Ocean, 5 of which were common to those of Kikuchi & Nemoto (see Zoogeography of the Aristeidae and Benthescymidae).

***Benthescymus investigatoris* Alcock & Anderson, 1899 (Fig. 12)**

Benthescymus investigatoris Alcock & Anderson, 1899a: 282, 1899b: pl. 41, fig. 2; Alcock 1901: 44; Rathbun, 1906: 906; Balss, 1927: 247, fig. 1; Burkenroad, 1936: 49; Anderson & Lindner, 1945: 298; Crosnier, 1978: 21, pls. 7c-d, 8c-d, 9, 10, 1984: 20, 1985: 857, 1989: 41, 1994a: 351, 1994b: 368; Hayashi, 1983d: 440, fig. 61; Kensley et al., 1987: 276; Kikuchi & Nemoto, 1991: 88, figs 16, 17.

Benthescymus investigatoris Borradaile, 1910: 258.

Benthescymus Investigatoris de Man, 1911: 5, 14; 1913: pl. 1, fig. 1.

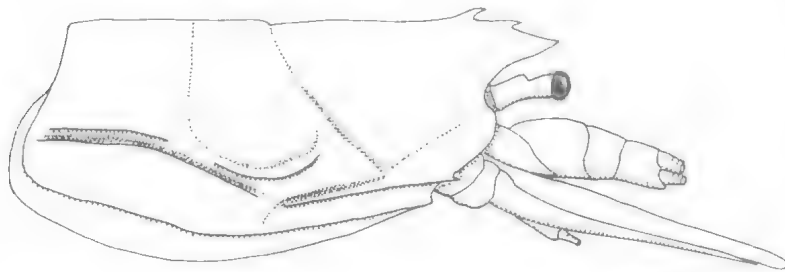


FIG. 12. *Benthescymus investigatoris* Alcock & Anderson, 1899 AMP39937, 27°59' S, 162°48' E, 1250m, ♂, 16.5mm.

MATERIAL. AMP39937, 28°S 163°E, 1250m, 6♂, 15-16.5mm, 5♀, 12.5-15mm; QMW13483, 17°45'S 148°E, 1115m, 2♂, 14, 18mm, 6♀, 14-21mm; QMW13447, 17°19'S 147°47'E, 1100m, ♀, 20mm.

DIAGNOSIS. Rostrum reaching about half the cornea, with 2 teeth and a minute bump in the position of a third, more posterior tooth; postrostral carina ending at the cervical sulcus. Antennal and hepatic spines absent; orbito-antennal sulcus present; branchiostegal spine prominent, raised above the surface of the carapace, set back just behind its margin and continuous with a prominent hepatic carina, which extends as far as the branchiocardiac carina; both carina and sulcus well defined.

Cervical sulcus deep, with a shallow notch where it crosses the mid-dorsum. A posthepatic carina and sulcus present, the sulcus turning towards the dorsum, which it crosses without a notch, at about 0.6 the length of the carapace; the accompanying carina interrupted at this level, but continuing parallel to the branchiocardiac sulcus. A dorsal carina clearly defined on abdominal somites 5 & 6, a barely defined carina on the posterior of somite 4; that of somite 5 ending in a small spine. Eye small, with brown pigment; pereopod 1 with a subdistal movable spine on the merus; rudimentary exopods on all pereopods. Petasma with dorsolateral lobule distally entire and semicircular, with thickened rim, ventral costa prominent and reaching almost as far as the dorsolateral lobule. Thelycum with a triangular prominence on the sternum of thoracic somite 6, the sternum of thoracic somite 7 a rounded projection with anterior edge w-shaped, that of somite 8 with two lateral circular indentations.

REMARKS. Of the 20 specimens examined, 11 (of both sexes and little different in size) did not have a well-defined dorsal carina on abdominal somite 4, but were otherwise valid *B.*

investigatoris. Thus this appears to be a variable character in this species.

DISTRIBUTION. E Australia 10-34°S; Lord Howe Rise 28°S 163°E; WA 29°05'S 113°14'E; Northwest Shelf 13°06'S 122°18'E; 879-1250m. Known range: throughout the Indo-West Pacific E coast of Africa, through the Indian Ocean, Indonesia, Australia, Philippines,

Japan, Hawaii, Fiji, Wallis & Futuna Islands, 580-1690m. A common benthescymid throughout its range; one trawl from the Cidaris' off NE Queensland included over 150.

***Benthescymus urinator* Burkenroad, 1936**

Benthescymus urinator Burkenroad, 1936: 29, figs 4, 5, 8, 9, 17, 18, 22, 32, 33, 39, 40, 45. Crosnier, 1985: 843, fig. 2; Kikuchi & Nemoto, 1991: 67, figs 4,5.

Benthescymus brasiliensis Bate, 1881: 191, 1888: 332 [part].

Benthescymus moratus Rathbun, 1906: 907.

DIAGNOSIS. Rostrum reaching about as far as the eye, tapering to the tip, with 2 fairly prominent dorsal teeth, with indications of a third; posterior tooth behind the margin of the

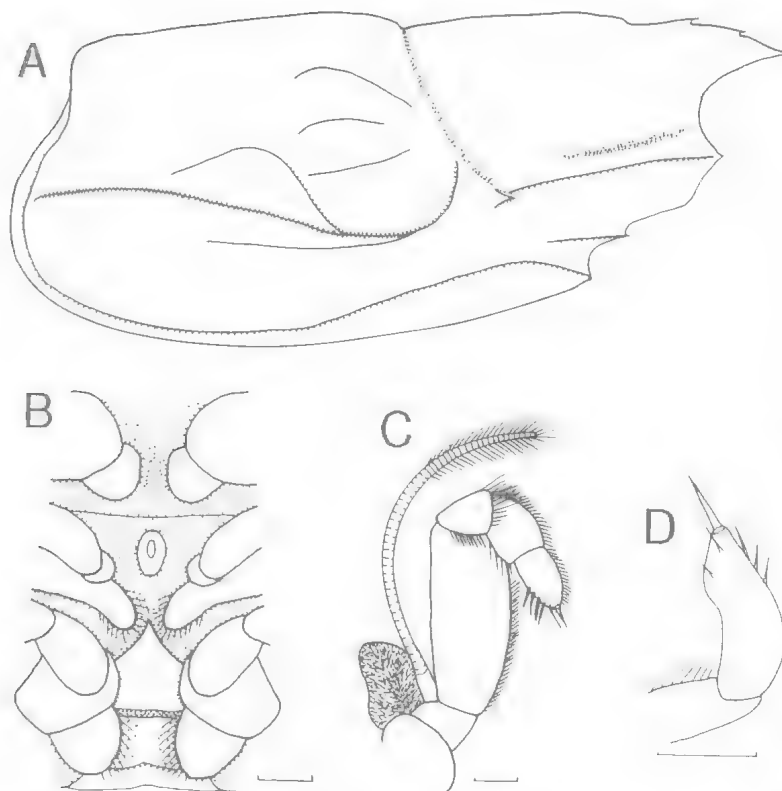


FIG. 13. *Benthescicymus urinator howensis* sp. nov. AM P40648, Lord Howe rise 28°44'S, 161°54'E, 1325m, ♀, 22mm. A, carapace; B, thelycum; C, maxilliped 2; D, maxilliped 3 dactyl. (Scalebar = 1mm)

carapace. Antennal spine acute, hepatic spine well developed; branchiostegal spine prominent, situated on the margin of the carapace and with a short carina. Cervical sulcus deep, notching the mid-dorsum and with a lower posterior branch which joins the branchiocardiac sulcus, the anterior branch reaching as far as the hepatic spine; branchiocardiac carina prominent; postcervical sulcus obscure; marginal carina well developed. Abdominal somites 4-6 carinate, each ending in a small spine; sixth somite more than twice as long as the fifth. Mandibular palp 2-segmented, basal segment 1.5 times the length and much broader than the distal segment, cutting edge of mandible straight with a small anterior tooth; endopod of second maxilla with long apical spine and seven long curved spines on the outer edge of the tip and a row of smaller spines on the inner edge; merus of second maxilliped expanded, length/width ratio 2.5, dactyl with 6 strong marginal spines; dactyl of third maxilliped broadest at its midpoint, tapering distally with 1 large spine at the tip.

Thelycum with inflated sternal plate on thoracic somite 8, a strong groove between sternites 7 & 8, sternite 7 with a prominent triangular projection, the apex directed anteriorly, a conical projection on somite 6.

REMARKS. Two ♂♂ and 2 ♀♀ (holotype and paratypes) were collected by the HMS Challenger' (Station 184) in the eastern approaches to Torres Strait. Kikuchi & Nemoto (1991) note that only 13 specimens have been collected in the Indo-West Pacific, so it appears to be uncommon, although widely distributed. All specimens are lodged in overseas museums and thus were not available (see, however, Fig. 13, *B. urinator howensis* sp. nov.). As it is a Group 1' benthescicymid it may be easily separated from the relatively common *B. investigatoris*.

DISTRIBUTION. Australia, Torres Strait approaches, 2560m. Known range: Indian Ocean, SW and N Pacific Oceans, 2500-4200m.

***Benthescicymus urinator howensis* sp. nov.**
(Fig. 13A-D)

MATERIAL. AM P40648, Lord Howe Rise, 28°44'S 161°54'E, 1325m, 2♀, 22, 24mm.

DISCUSSION. The above description for *B. urinator* (see also Crosnier, 1985, Fig. 2a, Kikuchi & Nemoto, 1991, figs 4, 5a) fits these specimens exactly in all respects except for the armature of the abdomen. They lack a posterior-medial spine of abdominal somite 4, which is a diagnostic feature of *B. urinator*, Crosnier (1985) remarking that this spine is the largest of the 3 abdominal spines. Unfortunately, the larger specimen is in poor condition and appears to lack a spine even on the fifth somite, but the 22mm specimen has a minute, but definite spine in this position, as well as a prominent spine on the sixth somite (both have a carina on the fifth

and sixth somites, but only a feeble indication of a carina on the fourth). As such it keys out as *B. seymouri*, which is obviously incorrect. Since the armature and carination of the abdominal somites are regarded as sufficiently stable to be used as key characters at both the specific and generic levels, these specimens may warrant the status of a new species. However, *B. urinator* is a rare species and the abdominal armature may be more variable than has been supposed. This plus the limited amount of material (only one relatively undamaged specimen) indicates that the erection of a new species would be unwarranted at this stage. Rather than designate it *Benthesicymus* sp.⁷ or *Benthesicymus* cf. *urinator*, in view of its close similarity to *B. urinator*, I prefer to assign it provisionally to a new subspecies.

Gennadas Bate, 1881

Gennadas Bate, 1881: 171, 191; 1888: 339; Alcock, 1901: 45; de Man, 1911: 15; Kemp, 1913: 60; Calman, 1925: 3; Balss, 1927: 248; Burkenroad, 1936: 59; Anderson & Lindner, 1943: 291; Barnard, 1950: 627; Kensley, 1971: 272; Crosnier, 1978: 33; Hayashi, 1984a: 18; Squires, 1990: 26; Pérez Farfante & Kensley, 1997: 63.

Amalopenacus Smith, 1882: 86.

Pasiphodes Filhol, 1885: pl 3.

DIAGNOSIS. Rostrum short, with a single dorsal tooth, not reaching as far as the cornea of the eye; adrostral carina absent, postrostral carina usually present. Antennal angle acute, narrowly rounded; infra-antennal angle demarcating a deep emargination of the carapace. A branchiostegal spine usually present on the inner edge of this emargination, branchiostegal carina present. Cervical and postcervical sulci present, both reaching the dorsal midline; a weak hepatic carina present. Only abdominal somite 6 with a dorsal carina; telson apically truncate, with a single pair of movable lateral spines. Second and third segments of antennular peduncle slightly expanded; exopod of first maxilliped without distal segmentation. Dactyli of pereopods 4 & 5 slender, uniarticulate. Petasma with distal margin divided into external, median and internal lobes; accessory lobe always present; thelycum variable, but with small shallow seminal receptacles at the base of pereopod 3, with either paired openings or a common median opening.

REMARKS. Seventeen species of *Gennadas* world wide have been described of which 5 appear to be restricted to the Atlantic and 1 to the E Pacific, but most of the remainder have been recorded world wide. The following are Indo-West Pacific species: *G. bouvieri*, *capensis*, *crassus*, *gilchristi*, *incertus*, *kemp*i, *parvus*,

propinquus, *scutatus*, *sordidus*, *tinayrei*. *G. parvus* Bate, 1881 has not yet been recorded from Australia, but in view of its wide distribution probably occurs here. *G. crassus* Tirmizi, 1960 has been recorded only from Zanzibar; *G. sordidus* Kemp, 1910 appears to be restricted to the NW Indian Ocean: the Arabian Sea, Gulf of Aden and Gulf of Oman. Neither of these species is included in the key below.

Gennadas species are soft and mostly < 10 mm CL; the features of the carapace and abdomen are closely similar and they would be extremely difficult to identify were it not for their very distinctive genitalia. The following keys use only features of the latter, with separate keys for males and females.

KEY TO THE INDO-WEST PACIFIC SPECIES OF GENNADAS

Adult male petasmas:

1. Median lobe undivided 2
Median lobe divided 4
2. External lobe divided by closely approximate blunt lobules *G. tinayrei*
External lobe undivided or with a small acute medial process 3
3. Accessory lobe bipartite *G. capensis*
Accessory lobe a single flap *G. kemp*i
4. Lobules of external lobe elongate, subequal, slender *G. incertus*
Lobules of external lobe not elongate, subequal, slender 5
5. Lobules of median lobe hooked *G. bouvieri*
Lobules of median lobe not hooked 6
6. Accessory lobe a mere ridge *G. parvus*
Accessory lobe well developed 7
7. Apex of internal lobe acute *G. gilchristi*
Apex of internal lobe rounded 8
8. Inner lobule of median lobe apically acute. *G. propinquus*
Inner lobule of median lobe apically truncate. *G. scutatus*

Adult female thelyca:

1. A posteriorly directed tongue-like projection on thoracic sternite 5 *G. tinayrei*
No tongue-like posterior projection on thoracic sternite 5 2
2. No obvious thelycal plate on thoracic somite 8 *G. capensis*
A well-developed thelycal plate on somite 8 3
3. Thelycal plate on thoracic somite 8 with broad rounded anterior extension reaching sternite of somite 6 *G. scutatus*
Thelycal plate on thoracic somite 8 not reaching the sternite of somite 6 4
4. Thelycal plate on thoracic somite 8 broad, anteriorly notched or indented and overlapping part of somite plate 7 *G. incertus*
Thelycal plate on thoracic somite 8 not indented anteriorly and not overlapping plate 7 5

5. Thelycal plate on thoracic somite 8 with two slender antero-lateral projections *G. bouvieri*
Thelycal plate on thoracic somite 8 without two slender antero-lateral projections 6
6. Thelycal plate on thoracic somite 7 with two medial anterior projections *G. gilchristi*
Thelycal plate on thoracic somite 7 without two anterior projections 7
7. A leaf-like process arising between the coxae of pereopods 3 & 4 and medially directed *G. parvus*
No leaf-like process arising between the coxae of pereopods 3 & 4 8
8. Thelycal plate on thoracic somite 7 W-shaped *G. propinquus*
Thelycal plate on thoracic somite 7 rectangular. *G. kemp*

***Gennadas bouvieri* Kemp, 1909**
(Fig. 14A-C)

Gennadas bouvieri Kemp, 1909: 726, pl. 74, fig. 1-4, pl. 75, fig. 6-7, 1910: 179; Burkenroad, 1936: 80; Anderson & Lindner, 1945: 293; Tirmizi, 1960: 360, figs 40d, 48e, 70-75; Kensley, 1968: 302, 1971: 273, fig. 1, 1972: 12, figs 4c, 6a; Roberts & Pequegnat, 1970: 36, figs 3-2B, 3-3C; Aizawa, 1974: 22, fig. 14; Crosnier, 1978: 34, figs 15a, 18a-b, 1994a: 352; Griffiths & Brandt, 1983: 179; Hayashi, 1984b: 140, fig. 66a-b; Kensley et al., 1987: 276.
Gennadas parvus Bate, 1881: 192 [part], 1888: 340 [part], pl. 59; Wood-Mason & Alcock, 1891a: 189 [part], 1891b: 286 [part]; Alcock, 1901: 46 [part].
Gennadas elegans Lenz & Strunck, 1914: 310 [part].
Amalopenaeus Alcocki Balss, 1927: 266, fig. 30.
Amalopenaeus Bouveri Balss, 1927: 267.

MATERIAL. AM P32892, 33°28'S 152°34'E, 641m, ♂, 8.5 mm, 7♀, 6.5-8.8mm (4♀, 6.5-7.2mm immature); AMP32895, 33°20'S 152°32'E, 366m, 2♂, 8.0mm, ♀, 8.2mm.

DESCRIPTION. Antennal angle and infra-antennal angles acute, but blunt. Petasma with external lobe divided into 2 broad, bluntly pointed lobules; median lobe broad with wide distal notch, the 2 lobules acute and inwardly

hooked; inner lobe much shorter than the median lobules, with numerous cincinnuli; accessory lobe large, leaf-shaped. Thelycal plate on thoracic somite 8 with slender processes on its anterolateral corners; the shield-shaped plate on somite 7 attached anteriorly to the plate of the somite 6, with rounded flap opening posteriorly and a small process on either side.

Colour. Uniformly red.

REMARKS. The hooked lobules of the median petasmas and the slender projections of the ♀ 8th thoracic sternite readily distinguish this species. Griffiths & Brandt (1983) recorded *G. bouvieri* at the edge or outside a warm-core eddy, where it appeared to be mesopelagic, but it was uncommon.

DISTRIBUTION. E Australia 17-39°S, 250-1988m. Known range: Indian Ocean; Indonesia; Arafura Sea; E Australia; Philippines; Japan; northwest Pacific; New Caledonia; Wallis and Futuna Islands, Eastern Pacific, Atlantic Ocean, 0-1115m, mostly 500-650m.

***Gennadas capensis* Calman, 1925**
(Fig. 15A-C)

Gennadas capensis Calman, 1925: 5, pl. 1, figs 1-2; Burkenroad, 1936: 67, figs 51, 53; Anderson & Lindner, 1945: 292; Barnard, 1950: 630, figs 118e-f; Roberts & Pequegnat, 1970: 34, fig. 3-2A; Kensley, 1971: 277, fig. 3; Abbes & Casanova, 1973: 268, fig. 5; Crosnier, 1978: 36, fig. 18c, 1985: 860, 1994b; Hayashi, 1984b: 141, fig. 66c-d; Kensley et al., 1971: 277, fig. 3, 1987: 277.

MATERIAL. AM P32880, 33°19'S 152°25'E, 640m, 5♂, 9.0-10.5mm, 7♀, 8.0-9.5mm; AMP32882, 33°28'S 152°34'E, 641m, 5♂, 10.2-13.2mm, 3♀, 9.1-12.0mm.

DIAGNOSIS. Antennal and infra-antennal angles acute. Lobes of the petasma not divided

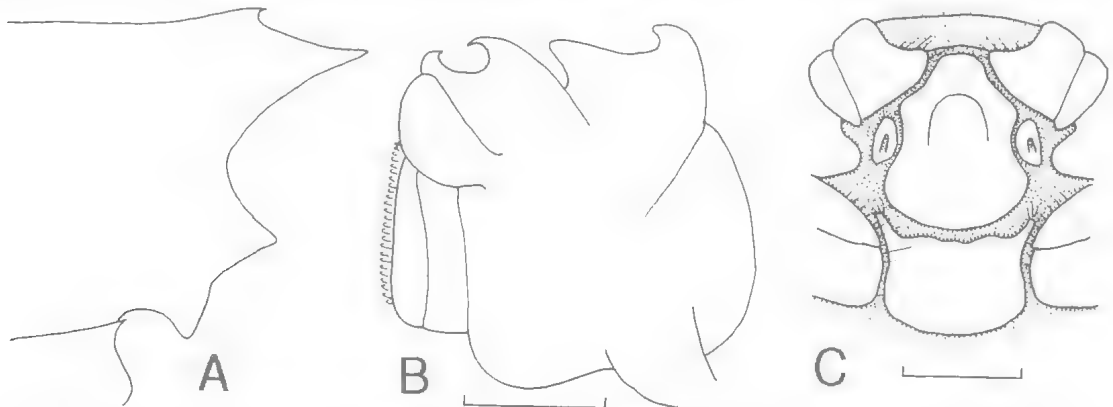


FIG. 14. *Gennadas bouvieri* Kemp, 1909 AMP32895, 33°20'S 152°32'E, 366m. A, ♂, 8 mm, anterior carapace; B, dorsal right half of petasma; C, ♀, 8.5 mm, thelycum. (Scalebar = 1 mm).

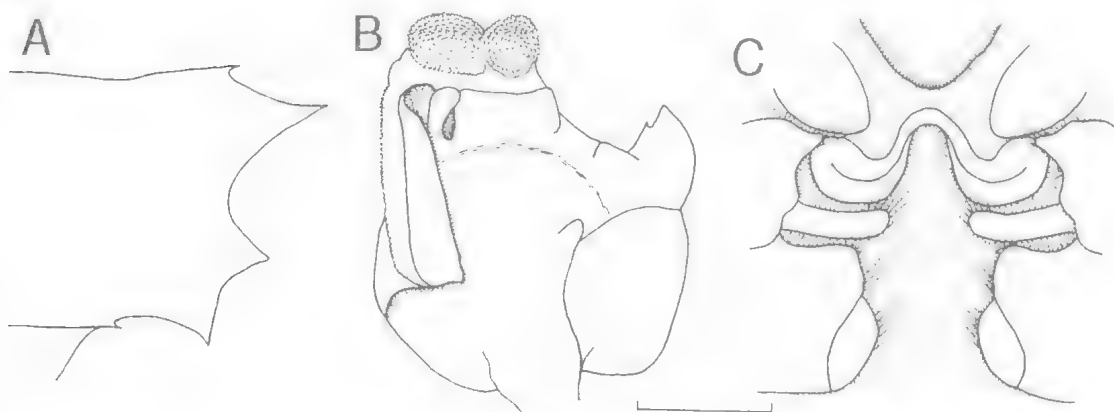


FIG. 15. *Gennadas capensis* Calman, 1925 AM P32880, 33°19'S 152°25'E, 640m. A, ♂, 10.5mm, anterior carapace; B, dorsal right half of petasma; C, ♀, 12mm, thelycum. (Scalebar = 1mm).

distally, but the external lobe with a small acute process on the medial margin; median lobe truncate and shorter than the adjacent lobes; inner lobe indented distally and covered with cincinnuli; accessory lobe divided, the inner lobule club-shaped, the outer truncate. Thelycal plate of thoracic somite 7 a prominent W-shape, median apex a rounded concave process; coxa of the pereopod 5 expanded and bilobed; coxa of the fourth with a slender elongate process; coxa of the third bluntly lobed; pereopod 3 with a pair of concave spoon-shaped processes posteriorly directed, meeting on midline.

Colour. Uniformly red.

REMARKS. This is one of the larger *Gennadas* (up to CL 13.2mm). A ♂ 7.5 mm CL was immature. *G. capensis* does not appear to be very common in Australian seas.

DISTRIBUTION. E Australia 22-39°S, 0-1988m, probably mesopelagic. Known range: W Indian Ocean; SE Australia; New Caledonia, Wallis and Futuna Islands, E Pacific, Atlantic Ocean, 0-2000m.

***Gennadas gilchristi* Calman, 1925**
(Fig.16 A-C)

Gennadas gilchristi Calman, 1925: 6, pl. 1, figs 3, 4; Burkenroad, 1936: 66, fig. 58; Barnard, 1950: 633, fig. 118g,h; Kensley, 1968: 301, 1971: 280, fig. 6; Griffith & Brandt, 1983: 179; Iwasaki & Nemoto, 1987: 5; Kensley et al., 1987: 277.

MATERIAL. AMP52815, 34°S 152°E, 950m, 14♂, 4.5-7.3 mm, 6♀, 5-7.3mm

DIAGNOSIS. Antennal and infra-antennal angles produced, apically rounded. Petasma with external lobe acute and a smaller lobule at its

outer base; median lobe with 2 diverging slender lobules; internal lobe acute; accessory lobe broadly rounded (Fig. 16B). Thelycum with a pair of anterior projections on thoracic 7 thelycal plate; a visible pair of circular seminal receptacles usually containing spermatophores just anterior to it; thoracic 8 thelycal plate apple-shaped, anterior margin extending over thoracic plate 7. Coxa of pereopod 3 expanded, bilobed, more prominent in ♀. (Fig.16C)

Colour. Uniformly red.

REMARKS. The distinctive dark circular spermatophores, red in preserved material, make ♀ *G. gilchristi* readily identifiable; the petasma is also distinctive. Kensley et al. (1987) noted that this is the commonest species in NSW collections that they examined. Collections in the Museum of Victoria, made with mid-water trawls off SE Australia confirm this. In some cases they seemed to be associated with trawls consisting largely of salps, being the only decapod crustaceans present. Griffiths & Brandt (1983) recorded *G. gilchristi* as the most abundant *Gennadas* species associated with the Tasman Sea warm-core eddies that they investigated. *G. gilchristi* was mostly on or outside the edge of the eddy at around 250m depth and thus appears to be mesopelagic. Griffiths observed (F. B. Griffiths, pers. com.) that the gut contents were commonly green algae, and suggested that the *Gennadas* had been feeding on salp faeces.

DISTRIBUTION. SE Australia, 33°-42°S, 200-1200m, S of Australia, to 45°S 115°-150°E, 0-1050m. Known range: off Cape Peninsula and W coast of S. Africa, Argulhas Basin, S Indian Ocean, SE Australia, New Caledonia, 0-3400m.

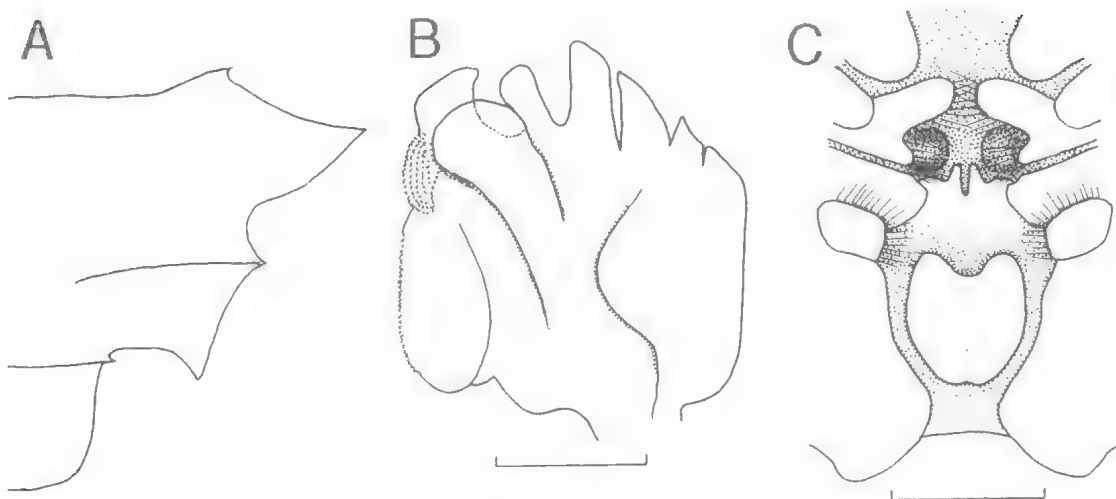


FIG. 16. *Gennadas gilchristi* Calman, 1925 AM P52815, 34°5'S 151°55'E, 950m. A, ♂, 7.3mm, anterior carapace; B, dorsal right half of petasma; C, ♀, 6mm, thelycum. (Scalebar = 1mm).

A mesopelagic species, preferred depth range appears to be 200-700m, mostly S of 30°S.

***Gennadas incertus* (Balss, 1927)**
(Fig.17A-C)

Amalopenacus incertus Balss, 1927: 265, figs 24-29.

Gennadas incertus Burkenroad, 1936: 66; Anderson & Lindner, 1945: 294; Tirmizi, 1960: 364, fig. 40e, 48f, 76-80; Percy & Forss, 1966: 1137; Kensley, 1971: 284, fig. 7, 1972: 12, 14, fig. 4i, 5j; Aizawa, 1974: 23, 44, figs 15, 29; Crosnier, 1978: 37, fig. 15b; Griffiths & Brandt, 1983: 179; Hayashi, 1984b: 141, fig. 66e; Kensley et al., 1987: 278.

MATERIAL. AM P35740, 33°20'S 152°32'E, 550m, 2♂, 7.2, 7.7mm, ♀, 8.0mm; AMP35741, 33°19'S 152°25'E, 640m, ♂, 7.4mm

DIAGNOSIS. Antennal angle blunt, infra-antennal angle quadrangular. External lobe of the petasma divided into two long tapering lobules, projecting well beyond the other lobes; median lobe divided into 2 rounded lobules, the outer relatively narrow, the inner lobule broad; inner lobe not divided, with cincinnuli along its inner margin; accessory lobe simple and reaching as far as the inner and median lobes. Thelycal plate on thoracic somite 8 indented anteriorly, and overlapping sternite 7 anteriorly; sternite 7 thelycal plate with acute anterolateral corners, posterolateral corners with rounded processes extended anteriorly; somite 6 with large concave plate.

Colour. Body generally red, paling anteriorly and posteriorly; thoracic appendages 2-5 dark red

with purplish spots; pleopods pale red with dark purple spots.

REMARKS. Kensley (1971) described and a small posterior notch on the sternite of thoracic somite 8, which he used in his key to distinguish *G. incertus*. Liu & Zhong (1986, pl. 24, fig. 5) also showed a small indentation, but no trace of a notch could be found on ♀♀ from SE Australia. Crosnier (1978, fig.15b) did not show any posterior indentation. It therefore does not appear to be a reliable distinguishing feature. Griffiths & Brandt (1983) record this species associated with the edge of a warm-core eddy in the Tasman Sea, probably mesopelagic, but it was not common.

DISTRIBUTION. E Australia, 17-34°S, 220-1406m. Known range: Indian Ocean, Australia, New Caledonia, Japan, NW & E Pacific, SE Atlantic, 100-1406m (diurnal vertical migration).

***Gennadas kemp* Stebbing, 1914**
(Fig.18A-C)

Gennadas kemp Stebbing, 1914: 283, pl. 27; Calman, 1925: 4; Burkenroad, 1936: 68, figs 52, 54; Barnard, 1950: 630, figs 118a-d; Kensley, 1971: 285, fig. 8; Iwasaki & Nemoto, 1987: 6; Kensley et al., 1987: 278.

MATERIAL. AMP32914, 33°31'S 152°20'E, 550m, ♂, 9.1mm; P32915, 33°19'S 152°25'E, 640m, 2♀, 9.2, 10.1mm.

DIAGNOSIS. Antennal and infra-antennal angles rounded. Petasma with external, median and internal lobes undivided; external lobe acute; median lobe broad and truncate; internal lobe

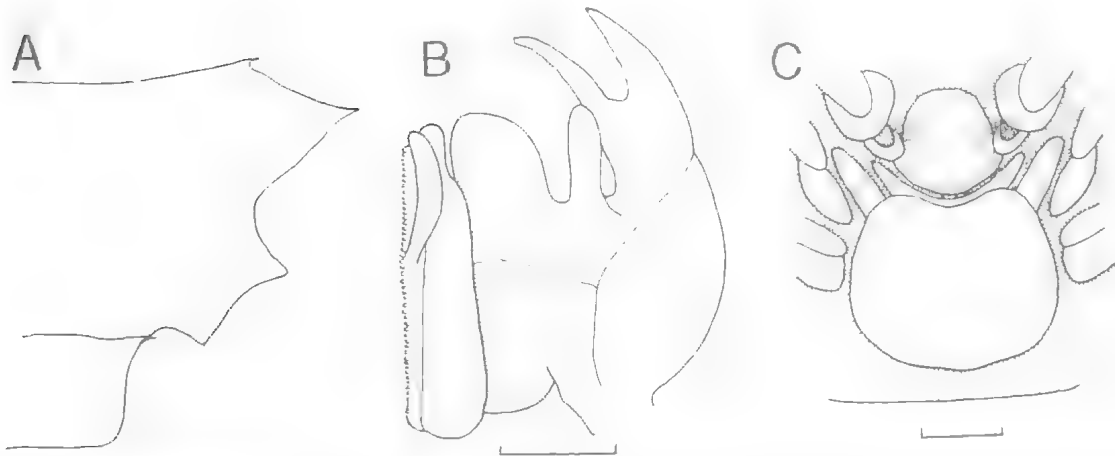


FIG. 17. *Gennadas incertus* Balss, 1927. AMP35740, 33°20'S 152°32'E, 366m. A, ♂, 7.7mm, anterior carapace; B, dorsal right half of petasma; C, ♀, 8mm, thelycum. (Scale bar = 1mm).

truncate, with rounded process bearing cincinnuli; accessory lobe a simple rounded flap not reaching as far as the internal lobe. Thelycal plate on the thoracic somite 8 hexagonal; that on sternite 7 subrectangular, with concave anterior edge, and that on sternite 7 triangular with apex directed anteriorly.

DISTRIBUTION. S Australia 32°-42°S, 550-640m, Antarctic Ocean (S of Australia, between 115°-150°E) down to 61°27'S, 0-1050m, probably mesopelagic. Known range: SE Indian Ocean, SE Australia, Antarctic Ocean, New Caledonia, SE Atlantic Ocean, 0-3400m; only recorded S of 32°S.

Gennadas propinquus Rathbun, 1906 (Fig. 19A-C)

Gennadas propinquus Rathbun, 1906: 907, fig. 61a, b; Burkenroad, 1936:66, 83; Anderson & Lindner, 1945: 295; Pearcey & Forss, 1966: 1137; Kensley, 1969: 167, fig. 9; Aizawa, 1974: 24, figs 17-19; Crosnier, 1978: 38, figs 16b, 18d-e, 1989: 41, 1994b: 369; Hayashi, 1984a: 142, fig. 66h; Liu & Zhong, 1986: 60, fig. 25; Kensley et al., 1987: 278.

Gennadas clavicarpus de Man, 1907: 144 [part], 1911: 19 [part], 1913: pl. 1, figs 3, 3a-c, pl. 2, fig. 3h,j, 1922: 3, pl. 1, fig. 1; Balss, 1927; Boone, 1930: 129, pl. 45 (♀ only); Irmizli, 1960: 353, figs 40c, 48c, 58-66; Kensley, 1971: 278, fig. 4; Griffiths & Brandt, 1983: 179.

Gennadas alcocki Kemp, 1910: 174, pl. 13: 1913: 62, pl. 7 (♀ only).

Gennadas scutatus Kemp, 1910: 178, pl. 13, figs 9, 10.

Gennadas scutatus indicus Kemp, 1913: 62 (♂♂ only).

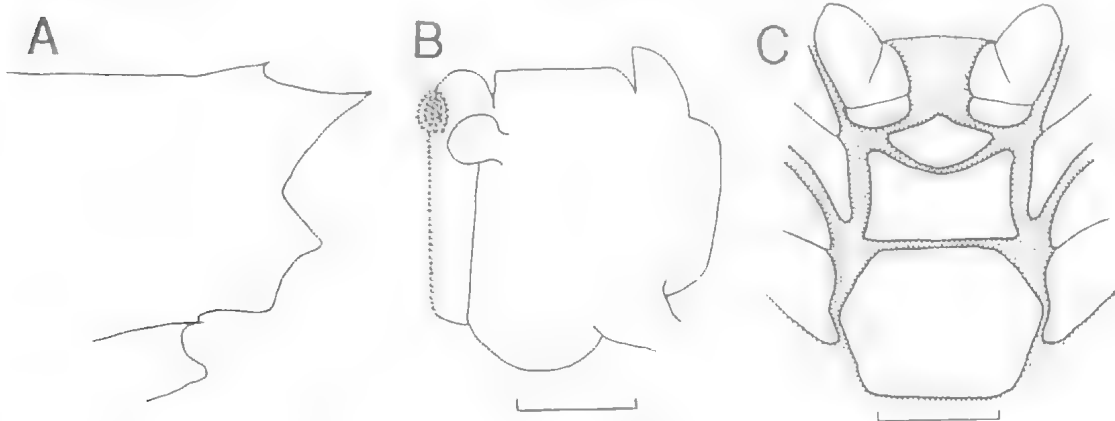


FIG. 18. *Gennadas kemp* Stebbing, 1914, AMP32915, 33°19'S 152°25'E, 640m. A, ♂, 10.1mm, anterior carapace; B, AMP32914, 33°31'S 152°20'E 550m, ♂, 9.1mm, dorsal right half of petasma; C, ♀, 8mm, thelycum. (Scale bar = 1mm).

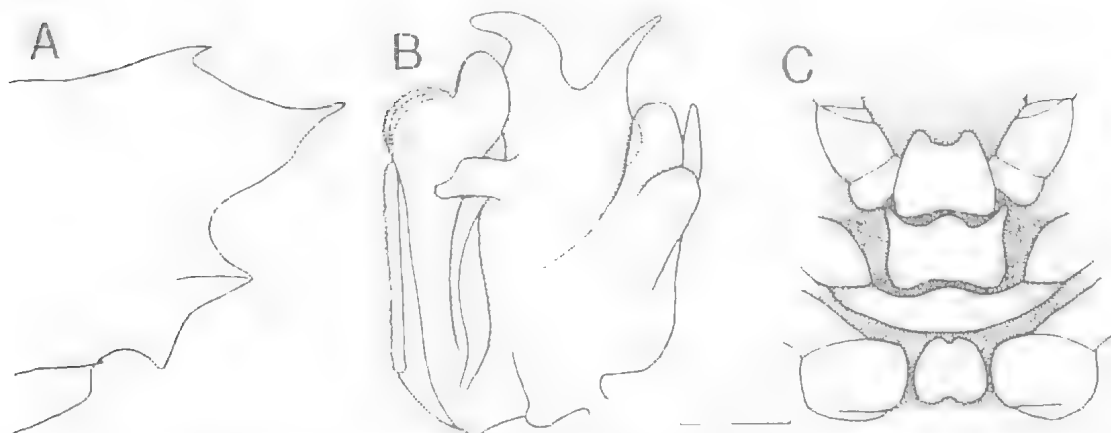


FIG. 19. *Gennadas propinquus* Rathbun, 1906 AM P32904, 33°20'S 152°32'E, 366m. A, ♂, 9.5mm, anterior carapace; B, dorsal right half of petasma; C, AM P32903, 33°17'S 152°31'E, 92m, ♀, 8.25mm, thelycum. (Scalebar = 1mm).

Amalopenaeus scutatus indicus Balss, 1927: 259, fig. 13.
Amalopenaeus clavicularis Balss, 1927: 267.

MATERIAL. AMP32903, 33°17'S 152°32'E, 92m, ♂, 6.2mm, 5♀, 5.1-8.2mm; AMP32904, 33°20'S 152°32'E, 366m, 5♂, 5.4-9.5mm.

DIAGNOSIS. Antennal and infra-antennal angles blunt. Petasma with the 3 lobes divided apically; the outer lobe with outer lobule acute and slender, inner lobule rounded; median lobe with both lobules prominent, apically acute; inner lobe with both lobules rounded, with cincinnuli; accessory lobe a simple flap. Thelycum with ovate plate on the sternum of thoracic somite 8, slightly indented anteriorly and posteriorly; thoracic somite 7 with a w-shaped plate, closely applied to the sub-triangular plate of the somite 6; the latter with indented anterior apex, openings of seminal receptacles at its base.

Colour. Body generally red, paling towards the anterior and posterior regions; thoracic appendages 2-5 dark red with purplish spots; pleopods pale red with dark purple spots at the base of each.

REMARKS. Griffiths & Brandt (1983) record this species (as *G. clavicularis*) at the edge and inside a warm core eddy in the Tasman Sea, but it was not abundant.

DISTRIBUTION. E Australia, 17°-42°S, 150-950m. Known range: Indian Ocean, Arabian Sea, Gulf of Aden, Philippines, China Sea, NW Pacific, SE Australia, New Caledonia, Wallis and Futuna Islands, E Pacific, SE Atlantic, 0-1200 m; mesopelagic migrating from deeper water at night to 100-200m.

Gennadas scutatus Bouvier, 1906 (Fig. 20A-C)

Gennadas scutatus Bouvier, 1906b: 748; 1906d: 5, 9-12, figs 8, 13, 1908: 42, pl. 8, figs 1-16; Milne Edwards & Bouvier, 1909: 193, figs 10-12; Kemp, 1909: 27, 727, pl. 75, fig. 2, 1913: 61 (♀ only); de Man, 1911: 6, 15; Lenz & Strunck, 1914: 310, 341; Calman, 1925: 4; Burkenroad, 1936: 83, fig. 59, 1938: 59; Anderson & Lindner, 1943: 295; Barnard, 1950: 634, fig. 1180-p; Tirmizi, 1960: 342, 346, 357, 358, figs 40c, 48d, 67-69; Belloc, 1961: 8; Crosnier & Forest, 1969: 549; 1973: 281, figs 94a, 95a, b, 1973; Roberts & Pequegnat, 1970: 39, fig. 3-1A; Kensley, 1971: 288, fig. 10, 1972: 12, 16, fig. 4d, 6g; Aizawa, 1974: 26, fig. 20; Crosnier, 1978: 43, fig. 17a, 1984: 20, 1994b: 369; Griffiths & Brandt, 1983: 179; Kensley et al., 1987: 279.

Gennadas clavicularis de Man, 1907: 145 [part], 1911: 19 [part], 1913: pl. 1, fig. 3f, g, pl. 2, fig. 3k; Boone, 1930: 129 (♂ only).

Amalopenaeus scutatus Balss, 1927: 258, figs 11, 12.

MATERIAL. AMP32913 33°17'S 152°31'E, 92m, ♂, 6.6mm.

DIAGNOSIS. Antennal and infra-antennal angles acute. Petasma with external lobe divided into 2 short rounded lobules; median lobe with slender outer lobule, the inner lobule broad with a small accessory lobule on its outer margin; internal lobe divided into 2 rounded inward-facing lobules, covered with cincinnuli; accessory lobe a simple triangular flap. Thelycal plate on thoracic somite 8 with a wide rounded anterior flap extending to cover about half sternite 6; sternite 6 thelycal plate triangular, with paired seminal receptacles at its base; sternite plate 7 a wide, flattened triangle; coxae of pereopod 4 with 4-5 inwardly-directed stout setae.

Colour. Uniformly red.

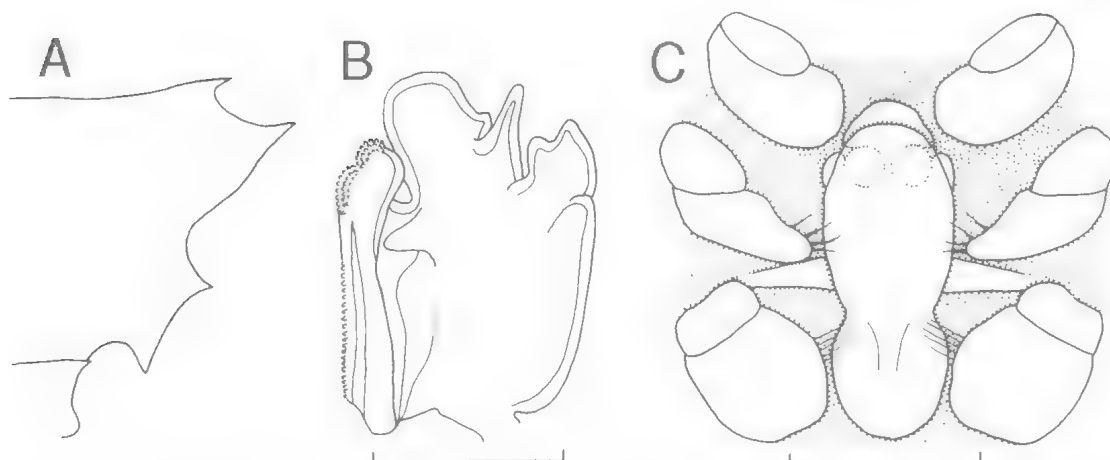


FIG. 20. *Gennadas scutatus* Bouvier, 1906, AMP32913, 33°17'S 152°31'E, 92m. A, ♀, 6.5 mm, anterior carapace; B, ♂, 5.3mm, dorsal right half of petasma. C, ♀, 6.5mm, thelycum. (Scale bar = 1mm).

REMARKS. Griffiths & Brandt (1983) recorded *G. scutatus* on the edge of a warm-core eddy in the Tasman Sea, but it was uncommon.

DISTRIBUTION. E Australia 17-38°S, 92-1192m. Range: throughout Indo-West Pacific, E Pacific and Atlantic Oceans, 0-3400m, mesopelagic.

***Gennadas tinayrei* Bouvier, 1906**
(Fig. 21A-C)

Gennadas Tinayrei Bouvier, 1906d: 10, figs 2-4, 14; 1908: 48, pl. 1, fig. 4, pl. 10; 1922: 10; Burkenroad, 1936: 73, fig. 56.

Gennadas tinayrei Lenz & Strunck, 1914: 313; Sund, 1920: 29; Anderson & Lindner, 1945: 293; Tirmizi, 1960: 367, figs 40f, 81-83; Kensley, 1971: 290, fig. 12, 1972: 12, figs 4b, 5c; Abbas & Casanova, 1973: 67; Aizawa, 1974: 27, fig. 21; Crosnier, 1978: 44, figs 17b, 19d; Hayashi, 1984b: 143, fig. 66k, l; Kensley et al., 1987: 279.

Amalopenaeus tinayrei Sund, 1920: 29.

Amalopenaeus Tinayrei Balss, 1927: 252, fig. 2.

MATERIAL. AMP32889, 33°31'S 152°20'E, 550m, ♂, 6.2mm; AMP52827, 34°05'S 151°55'E, 950m, ♂, 6.3mm; 3♀, 7.1, 7.2, 7.3.

DIAGNOSIS. Antennal and infra-antennal angles acute. Petasma with external lobe slightly indented, edged with minute teeth and with a small lobule at its base; middle lobe broad and slightly convex; inner lobe with 2 rounded projections covered with cincinnuli; accessory lobe flattened and rounded in outline. Thelycal plate on thoracic somite 8 small and subrectangular; plate on the somite 7 a wide triangle with 2 rounded processes on either side of its apex, and just anterior to these a further 2 smaller rounded processes on the somite 6;

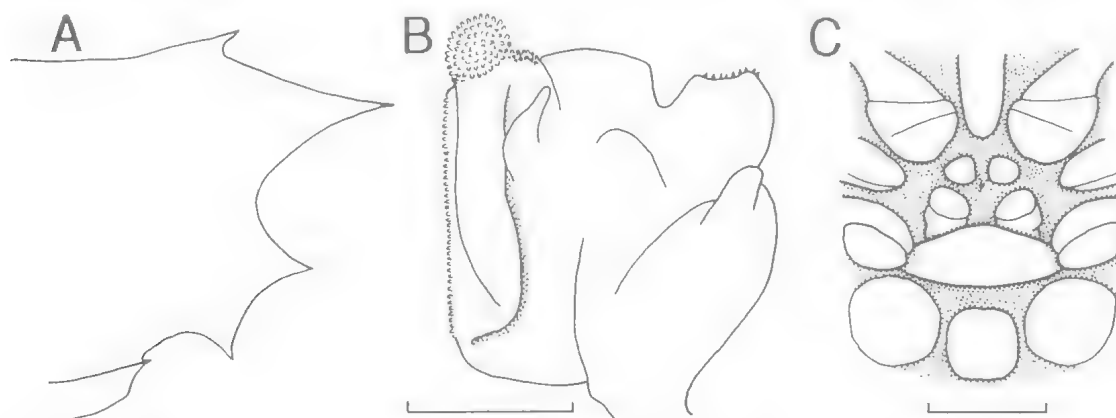


FIG. 21. *Gennadas tinayrei* Bouvier, 1906, AM P52827, 34°5'S, 151°55'E, 950m. A, ♀, 7.3 mm, anterior carapace. B, ♂, 6.3mm, dorsal right half of petasma. C, ♀, 7.3 mm, thelycum. (Scale bar = 1mm).

sternite of the somite 5 with a posteriorly directed tongue-like process.

Colour. Uniformly red.

DISTRIBUTION. SE Australia 33-42°S, 92-950 m. Known range: throughout the Indian Ocean, SE Australia, Japan, NW Pacific, Atlantic Ocean, 92-950, probably mesopelagic and uncommon.

ZOOGEOGRAPHY OF THE ARISTEIDAE AND BENTHESICYMIDAE

As the Aristeidae and Benthescymidae inhabit a zone from 0-5000m, to some extent their apparent distribution reflects the collecting methods that have been used in different parts of the world by various expeditions or fishery investigations. Often only benthic collectors have been used (trawls, sledges or dredges) and pelagic or even epibenthic species have been missed or collected adventitiously during shooting or retrieval of the net. Mid-water trawls have often shown that some species hitherto considered rare, are common. The ideal approach is to use various collecting devices as described by Kikuchi & Nemoto (1991). These included an opening-closing net, a mid-water trawl, baited traps and an Agassiz-type trawl. The first 3 were the most successful in collecting *Benthescymus* and enabled Kikuchi & Nemoto to distinguish bathy- and meso-pelagic species from predominantly benthic species. It is also of interest that of the 8 *Benthescymus* species recorded, the trawl collected only *B. investigatoris* and that only once!

The depth range for most of the Aristeidae is within a 200-2000m zone, with a few reaching 5000m or more. All species of Aristeidae have well-developed pleopods and like members of other penaeoid families are probably capable of swimming appreciable distances and may swim up and down in the water column. For example, Crosnier (1978) produced evidence that *Aristaeomorpha foliacea* undergoes a vertical diurnal migration. The depth range of other species suggests that this may not be an isolated case (e.g. *Hepomadus tener*, 765-5400m).

As shown by the increasing use of mid-water trawls over the last 40 years, the Benthescymidae are largely pelagic and even those classed as benthic probably spend a large part of their time in the water column. All are small, possess thin cuticles, have well-developed pleopods and probably have low density muscle and other tissues. Although some of the species, subsequently shown to be pelagic, have been

collected in bottom trawls, it must have been while the trawl was being shot or retrieved. Pelagic (bathy-, meso- and fully pelagic) genera are *Benthonectes*, *Gennadas* and probably all species of *Bentheogennema*. *Benthescymus brevirostris* and *B. carinatus* are also pelagic (Kikuchi & Nemoto, 1991). Thus the depth range recorded for these species may range from upper levels to 5000m.

Longitudinal distribution. Since the Aristeidae are predominantly benthic data collected from bottom trawls probably give a realistic picture of their distribution. In contrast, unless a variety of collecting methods have been used in a given area, the apparent distribution of the Benthescymidae may not give a true picture. This is certainly the case for Australian seas. Intensive deeper water trawling and later mid-water trawling off SE Australia has collected 8 species of *Gennadas*, some of which appear to be common or even abundant. None of these species had been collected in other parts of Australia until the Australian Institute of Marine Science 'Cidaris 1' expedition, which collected 4 *Gennadas* species, using various types of gear. As noted previously, of the species of *Benthescymus*, only *B. investigatoris*, *B. urinator* and a possible third species have been collected from Australian seas, but this is unlikely to be the true picture as Kikuchi & Nemoto (1991) recorded 8 species from the NW Pacific and Crosnier (1978, 1985) 8 from the western and central Indian Ocean, 5 of which were common to those of Kikuchi & Nemoto.

Given the provisos regarding collecting methods, it is obvious that the Aristeidae and Benthescymidae are generally more widely distributed than most of the remaining Penaeoidea. Of 25 species of Aristeidae 8 have been recorded in both the Indo-West Pacific and Atlantic Oceans, with *Hemipenaeus carpenteri*, *H. spinidorsalis*, *Plesiopenaeus armatus* in the E Pacific as well. Of the remaining 17 species, 7 range through the Indo-West Pacific, and 10 appear to be more localised. Among the 37 species of Benthescymidae, 14 are common to both the Indo-West Pacific and Atlantic Oceans, with 12 of these common to the E Pacific as well; an additional 3 are found through the Indo-West Pacific, and 20 have a more restricted range. A 'restricted range' may be due to misidentification, limited or inappropriate collection methods, or rarity of a species.

Latitudinal distribution. The pelagic species of the Benthescymidae appear to have the widest

latitudinal range. In the N Pacific the pelagic *Bentheogennema borealis* has been recorded in the S Bering Sea (around 57°N) where it is a relatively abundant mesopelagic inhabitant (Butler, 1980). *Bentheogennema burkenroadi* has been collected at 52°N off the coast of British Columbia and again is relatively abundant. No other penaeoids have been recorded in this region at such high latitudes and 45°N appears to be the approximate limit for other pelagic species. In the NW Atlantic *G. elegans* has been collected up to 57°N off the Labrador shelf, while *G. valens* has been recorded at 51°N in the northeastern Atlantic off Ireland (Squires, 1990). No other benthescymid species have been collected N of about 44°N (Squires, 1990). In the Southern Hemisphere the range is comparable with that of the N Pacific. *G. kemp*i was collected S of Australia as far as 61°27'S in the Antarctic Ocean (Iwasaki & Nemoto, 1987). Various midwater collecting devices were used with oblique tows from 700-1000m to surface. *G. kemp*i was collected at 10 stations, from 2-17 per station and thus it appears to be fairly abundant even at the highest latitudes of its range. The same cruise collected *G. gilchristi* around the Sub-Tropical Convergence at 45°S, but none beyond this latitude. It seems, therefore, that the majority of pelagic Benthescymidae are restricted to a zone between 45°N and 45°S, with a few species adapted to the lower temperatures of higher latitudes. Of the benthic Aristeidae and Benthescymidae the range appears to be a little less, mostly 40°N - 40°S.

The wide longitudinal distribution of many Aristeidae and Benthescymidae may be explained by lack of geographical barriers at depths of 1000m and more. The reason that the majority are confined to 40°N - 40°S is less obvious. It has been suggested for the Solenoceridae that this is due to the larvae in the upper water column being adapted to higher water temperatures (Dall, 1999). Thus in the Southern Hemisphere as the Subtropical Convergence zone is approached around 40°S, the upper water temperatures begin to fall sharply and so limits the southern distribution of the Solenoceridae. The same mechanism appears to apply to the Aristeidae and Benthescymidae and perhaps indicates a tropical origin for these families. However, not all species range through tropical or subtropical latitudes.

One aristeid species appears to be restricted to higher southern latitudes: *Austropenaeus nitidus*. It inhabits a zone 26° - 40°S from the S Atlantic

Ocean, South Africa, across the Indian Ocean (Amsterdam and St. Paul Islands) and across S Australia, where it appears to be common. It is likely that its longitudinal range is even wider. The mesopelagic *G. gilchristi* and *G. kemp*i have a N limit similar to that recorded for *Austropenaeus nitidus* (around 30°S), except that one *G. gilchristi* has been collected at 21°S by a midwater trawl off E New Caledonia. However, the abundance of *G. gilchristi* south of 33°S in E Australian waters suggests that this may be a stray from higher latitudes.

In conclusion, it appears that deep water Penaeoidea are less subject to the geographical barriers which influence the distribution of most of those penaeoid species that inhabit the continental shelf and its outer edges. This particularly applies to the pelagic Benthescymidae many of which have a wide longitudinal range with temperature as the major north and south latitudinal limiting factor. Significantly in this regard, 2 species of pelagic *Funchalia* (Penaeidae) are also cosmopolitan.

ACKNOWLEDGEMENTS

This work was made possible by a grant from the Australian Biological Resources Survey. My sincere thanks are due to the relevant Curators and/or Collections Managers of the following museums which I visited and which loaned material: The Australian Museum, Sydney, Penny Barents; The Museum of Victoria, Gary Poore and Vicky Barmby; The Museum of Tasmania, Hobart, Roger Buttermore; The ISR Munro Fish Collection, CSIRO Marine Laboratories, Hobart, Alistair Graham; The Queensland Museum, Brisbane, Peter Davie and John Short; The Museum of Tropical Queensland, Peter Arnold. Gavin Dally, Collections Manager of the Museum of Northern Territory also sent specimens on loan. I thank the Chief, Division of Marine Research, CSIRO for providing facilities at the CSIRO Marine Laboratories, Cleveland. I also thank Alain Crosnier, Muséum National D'Histoire Naturelle and Ken-Ichi Hayashi, Shimomoseki University of Fisheries for critically reading the manuscript and making a number of helpful suggestions.

LITERATURE CITED

- ABBES, R. & CASANOVA, J. P. 1973. Crustacés Décapodes pélagiques *Penaeidea* et *Caridea* récoltés par la "Thalassa" dans l'Atlantique ouest-africain. Revue des Travaux de l'Institut des Pêches maritimes 37: 257-290.

- AIZAWA, Y. 1974. Ecological studies of micronekton shrimps (Crustacea, Decapoda) in the Western North Pacific. *Bulletin of the Ocean Research Institute of the University of Tokyo* 6: 1-84.
- ALCOCK, A. 1899. A summary of the deep-sea zoological work of the Royal Indian Marine Survey Ship "Investigator" from 1884 to 1897. *Scientific Memoirs of the Medical Officer of the Army of India* 11: 45-93.
1901. A descriptive catalogue of the Indian deep-sea Crustacea Decapoda Macrura and Anomala in the Indian Museum. (Indian Museum: Calcutta).
- ALCOCK, A. & ANDERSON, A.R.S. 1894. Natural history notes from H.M. Indian Marine Survey steamer Investigator, Commander C.F. Oldham, R.N. Commanding. Series II, No. 14. An account of a recent collection of deep sea Crustacea from the Bay of Bengal and Laccadive Sea. *Journal of the Asiatic Society of Bengal* 63: 141-185.
1899. An account of the deep-sea Crustacea dredged during the surveying-season of 1897-98. Natural history notes from H.M. Royal Indian Marine Survey Steamer 'Investigator', commander T.H. Heming, R.N., commanding. Ser III, no. 2. *Annals and Magazine of Natural History* 7(3): 1-27, 278-292.
- ALCOCK, A. & McARDLE, A.F. 1901. Illustrations of the zoology of the Royal Indian Marine Surveying Steamer Investigator. Crustacea, pt. 9, 49-55 pl.
- ANDERSON, A.R.S. 1896. Natural history notes from the R.I.M. Survey Steamer "Investigator", Commander C. G. Oldham, R.N. commanding. Series II, No. 21. An account of the deep sea Crustacea collected during the season 1894-95. *Journal of the Asiatic Society of Bengal* 65: 88-106.
- ANDERSON, W.W. & LINDNER, M.J. 1945. A provisional key to the shrimps of the Family Penaeidae with especial reference to American forms. *Transactions of the American Fisheries Society* 73: 284-319.
- BALSS, H. 1925. Macrura der Deutschen Tiefsee-Expedition. 3. Natantia, Teil A. *Wissenschaften Ergebnisse der deutschen Tiefsee-Expedition auf dem Dampfer Valdivia* 20(5): 217-315.
1927. Macrura der Deutschen Tiefsee-Expedition. 3. Natantia, Teil B. *Wissenschaften Ergebnisse der deutschen Tiefsee-Expedition auf dem Dampfer Valdivia* 23(6): 245-275.
1957. Systematik. Bronn's Klassen und Ordnungen des Tierreichs 5(1)7. Decapoda 12: 1505-1672.
- BARNARD, K.H. 1947. Descriptions of new species of South African Decapod Crustacea, with notes on synonymy and new records. *Annals and Magazine of Natural History* (11) 13: 361-392.
1950. Descriptive catalogue of South African decapod Crustacea. *Annals of the South African Museum* 38: 1-837.
- BATE, C.S. 1881. On the Penaeidea. *Annals and Magazine of Natural History* (5)8: 169-196.
1888. Report on the Crustacea Macrura collected by H.M.S. Challenger during the years 1873-76. Report of the Scientific Results of the Challenger, 1873-76, Zool 24. xc+942 p. 2nd part CL pl.
- BELLOC, G. 1961. Catalogue des types de Décapodes du Musée océanographique de Monaco. *Bulletin de l'Institut océanographique*, Monaco 1212: 1-19.
- BOONE, L. 1930. Crustacea: Anomura, Macrura, Schizopoda, Isopoda, Amphipoda, Mysidacea, Cirrepedia, and Copepoda. Scientific results of the cruises of the yachts "Eagle" and "Alva", 1921-1928, William K. Vanderbilt commanding. *Bulletin of the Vanderbilt Marine Museum* 3: 221.
- BOUVIER, E.L. 1905. Sur les Pénéides et les Sténopides recueillis par les expéditions françaises et monégasques dans l'Atlantique oriental. *Comptes rendus hebdomadaires des Séances de l'Académie de Sciences*, Paris 140: 980-983.
- 1906a. Sur les *Gennadas* ou Pénéides bathypélagiques. *Comptes rendus hebdomadaires des Séances de l'Académie de Sciences*, Paris 142: 686-690.
- 1906b. Observations sur les Pénéides du genre *Haliporus* Sp. Bate. *Bulletin du Musée océanographique*, Monaco 81: 1-10.
1908. Crustacés Décapodes (Pénéides) provenant des campagnes de l'Hirondelle et de la Princesse Alice (1886-1907). Résultats des Campagnes scientifiques accomplies par le Prince Albert I de Monaco 33: 1-122.
1922. Observations complémentaires sur les Crustacés Décapodes (abstraction faite des Carides), provenant des campagnes de S.A.S. le Prince de Monaco. Résultats des Campagnes scientifiques accomplies par le Prince Albert I de Monaco 62: 1-106.
- BURKENROAD, M.D. 1936. The Aristaeinae, Solenocerinae and pelagic Penaeinae of the Bingham oceanographic collection, *Bulletin of the Bingham Oceanographic Collection* 5: 1-151.
1938. The Templeton Crocker Expedition. XIII. Penaeidae from the region of Lower California and Clarion Island with descriptions of four new species. *Zoologica* 23: 55-91.
- BUTLER, T.J. 1980. Shrimps of the Pacific coast of Canada. *Canadian Bulletin of Fisheries and Aquatic Sciences* 202: 1-280.
- CALMAN, W.T. 1925. On macrurous decapod Crustacea collected in South African waters by the S.S. 'Pickle'. Investigational reports of the Division of Fisheries, Union of South Africa. Report No. 4 for the year 1925. Special Report 3: 1-26.
- CROSNIER, A. 1978. Crustacés Décapodes Pénéides Aristidae (Benthescymidae, Aristidae, Solenoceridae). *Faune de Madagascar* 46: 1-197.
1984. Penaeoid shrimps (Benthescyminae, Aristaeinae, Solenocerinae, Sicyoniidae)

- collected in Indonesia during the Corindon II et IV expeditions. Marine Research in Indonesia 24: 19-47.
1985. Crevettes Pénéides d'eau profonde récoltées dans l'océan Indien lors des campagnes Benthedi. Safari I et II, MD 32/Reunion. Bulletin du Muséum national d'Histoire naturelle, Paris (4) 7: 839-877.
1989. Benthescymidae, Aristeidae, Solenoceridae (Crustacea Penaeoidea). 37-67. In J. Forest (ed.), Résultats des Campagnes Musorstom, Vol. 5. Mémoires du Muséum national d'Histoire naturelle (A) 144: 37-67.
- 1994a. Crustacea Decapoda: Penaeoidea récoltés lors de la campagne Karubar en Indonésie. Pp. 351-365. In Crosnier, A. (ed.) Résultats des Campagnes Musorstom, Vol. 12. Mémoires du Muséum national d'Histoire naturelle 161: 351-365.
- 1994b. Crustacea Decapoda: Penaeoidea à l'exclusion des Sicyonidae récoltés dans la zone économique des îles Wallis et Futuna lors de la campagne Musorstom 7. 367-373. In Crosnier, A. (ed.) Résultats des campagnes Musorstom, Vol. 12. Mémoires du Muséum national d'Histoire naturelle 161: 367-373.
- CROSNIER, A. & FOREST, J. 1969. Note préliminaire sur les Pénéides recueillis par l'"Ombango" au large du plateau continental, du Gabon à l'Angola (Crustacea Decapoda Natantia). Bulletin du Muséum national d'Histoire naturelle, (2) 41(2): 544-555.
1973. Les crevettes profondes de l'Atlantique oriental tropical. Faune tropicale 19: 1-409.
- DALL, W. 1991. Zoogeography of the Penaeidae. Memoirs of the Queensland Museum 31: 39-50.
1999. Australian species of Solenoceridae (Penaeoidea: Decapoda). Memoirs of the Queensland Museum 43(2): 553-587.
- DALL, W., HILL, B.J., RÖTHLISBERG, P.C. & STAPLES, D.J. 1990. The biology of the Penaeidae. Advances in Marine Biology 27. (Academic Press: London).
- DE FREITAS, A.J. 1985. The Penaeoidea of southeast Africa. II. The Families Aristeidae and Solenoceridae. Investigational Report No. 57, 69 pp. Oceanographic Research Institute, Durban.
- DE MAN, J.G. 1907. Diagnoses of new species of macrurous Decapod Crustacea from the Siboga Expedition. II. Notes from the Leyden Museum 29: 127-147.
1911. The Decapoda of the Siboga Expedition. Part 1. Family Penaeidae. Siboga Expedition Monographie 39a: 1-131.
1913. The Decapoda of the Siboga Expedition. Part 1. Family Penaeidae. Siboga Expedition Monographie 39a: Suppl., 1-X pl.
1922. On a collection of Macrurous Decapod Crustacea of the Siboga Expedition, chiefly Penaeidae and Alpheidae. The Decapoda of the Siboga Expedition. Siboga Expedition Monographie 39a: 1-51.
- DUVERNÖY, G.L. 1840. Note sur une nouvelle forme de branchies, découverte dans une espèce de Crustacé décapode macrour, qui devra former le type d'un genre nouveau (*Aristeus antennatus*, Nob.). Comptes rendus hebdomadaires des Séances de l'Académie de Sciences, Paris 11: 217-220.
- FAXON, W. 1893. Reports on the dredging operations off the west coast of Central America. Bulletin of the Museum of comparative Zoology at Harvard College 24(7): 149-220.
1895. The stalk-eyed Crustacea. Memoirs of the Museum of comparative Zoology at Harvard College 18: 1-292.
1896. Supplementary notes on the Crustacea. Bulletin of the Museum of comparative Zoology at Harvard College 30: 151-161.
- FILHOL, H. 1885. La vie au fond des mers. Les explorations sous-marines et les voyages du Travailleur et du Talisman. Bibliothèque de la Nature. (G. Masson: Paris).
- GREY, D.L., DALL, W. & BAKER, A. 1983. A Guide to the Australian Penaeid Prawns. (Department of Primary Production, Northern Territory: Darwin).
- GRIFFITHS, F.B. & BRANDT, B. 1983. Distribution of mesopelagic decapod Crustacea in and around a warm-core eddy in the Tasman Sea. Marine Ecology-Progress Series 12: 175-184.
- HANAMURA, Y. 1989. Deep-sea shrimps (Crustacea: Decapoda) collected by the R.V. "Soela" from Southern Australia. Bulletin of the Biogeographical Society of Japan 44: 51-69.
- HAYASHI, K.-I. 1983a. Prawns, shrimps and lobsters from Japan (11). Family Aristeidae (Aristeinae)-Genus *Aristeus*. Aquabiology 26 (V-3): 188-191.
- 1983b. Prawns, shrimps and lobsters from Japan (12). Family Aristeidae (Aristeinae)-Genera *Aristaeomorpha* and *Hepomadus*. Aquabiology (V-4): 280-283.
- 1983c. Prawns, shrimps and lobsters from Japan (13). Family Aristeidae (Aristeinae) - Genera *Hemipenaeus* and *Plestipenaeus*. Aquabiology 28 (V-5): 366-369.
- 1983d. Prawns, shrimps and lobsters from Japan (14). Family Aristeidae (Benthescyminae) - Genus *Benthescymus*. Aquabiology 29 (V-6): 438-441.
- 1984a. Prawns, shrimps and lobsters from Japan (15). Family Aristeidae (Benthescyminae) - Genus *Gemmadus* (1). Aquabiology 30 (VI-1): 18-21.
- 1984b. Prawns, shrimps and lobsters from Japan (16). Family Aristeidae (Benthescyminae) - Genus *Gemmadus* (2). Aquabiology 30 (VI-1): 140-145.
- IWASAKI, N. & NEMOTO, T. 1987. Pelagic shrimps (Crustacea: Decapoda) from the Southern Ocean between 150°E and 115°E. Memoirs of National

- Institute of Polar Research, Series E, Biology and Medical Science 38: 1-40.
- JOHNSON, J.Y. 1867. Descriptions of a new genus and a new species of macrurous decapod Crustaceans belonging to the *Penaeidae*, discovered at Madeira, Proceedings of the Zoological Society of London 1867: 895-901.
- KEMP, S.W. 1909. The Decapoda of the genus *Gennadas* collected by H.M.S. "Challenger". Proceedings of the Zoological Society of London 1909: 718-730.
1910. Notes on Decapoda in the Indian Museum. I. The species of *Gennadas*. Records of the Indian Museum 5(3): 173-181.
1913. Pelagic Crustacea Decapoda of the Percy Sladen Expedition in H.M.S. "Sealark". Transactions of the Linnaean Society of London (2) Zoology, 16(1): 1-190.
- KEMP, S.W. & SEYMOUR-SEWELL, R.B. 1912. Notes on Decapoda in the Indian Museum. III. The species obtained by R.L.M.S.S. "Investigator" during the survey season 1910-11. Records of the Indian Museum 7:15-32.
- KENSLEY, B.F. 1968. Deep-sea Crustacea from West of Cape Point, South Africa. Annals of the South African Museum. 50(12): 283-323.
1971. The genus *Gennadas* in the waters around Southern Africa. Annals of the South African Museum. 57(12): 271-294.
1972. Shrimps and prawns of Southern Africa. (South African Museum: Cape Town).
- KENSLEY, B.F., FRATER, H.A. & GRIFFIN, D.J.G. 1987. Deepwater decapod Crustacea from Eastern Australia (Penaeidea and Caridea). Records of the Australian Museum 39: 263-331.
- KIKUCHI, T. & NEMOTO, T. 1986. List of pelagic shrimps (Crustacea, Decapoda) from the western North Pacific. Bulletin of the Biogeographical Society of Japan 41(7): 51-60.
1991. Deep-sea shrimps of the genus *Benthescymnus* (Decapoda: Dendrobranchiata) from the western North Pacific. Journal of Crustacean Biology 11(1): 64-89.
- KOMAI, T. 1993. Deep-sea shrimps of the family Aristeidae (Decapoda: Dendrobranchiata) from northern Japan, with the description of a new species of the genus *Aristeus*. Crustacean Research 22: 21-34.
- KUBO, I. 1949. Studies on the penaeids of Japanese and its adjacent waters. J. Tokyo Coll. Fish. 36: 1-467.
- LENZ, H. & STRUNCK, K. 1914. Die Dekapoden der Deutschen Südpolar-Expedition 1901-1903. I. Brachyuren und Macruren mit Ausschluss der Sergestiden. Wissenschaftliche Ergebnisse der Deutsche Südpolar-Expedition. 15, Zoologie 7: 259-345.
- LIU, J.Y. & ZHONG, Z. 1986. Penaeoid shrimps of the South China Sea. (Agricultural Publishing House: Beijing).
- MIERS, E.J. 1878. Notes on the Penaeidae in the collection of the British Museum, with descriptions of some new species. Proceedings of the Zoological Society of London 1878: 289-310.
- MILNE-EDWARDS, H. 1837. Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux 2: 1-532.
- MILNE-EDWARDS, A. & BOUVIER, E.L. 1909. Les Pénéides et Sténopides. Memoirs of the Museum of comparative Zoology at Harvard College 27(3): 177-274.
- OKADA, Y., SAKAMOTO, I., AMANO, R. & TOMINAGA, Y. 1966. Preliminary report of the benthic biological survey in Suruga Bay. Journal of the Faculty of Oceanography of Tokai University 1966(1): 135-155.
- PEARCY, W.G. & FORSS, C.A. 1966. Depth distribution of oceanic shrimps (Decapoda: Natantia) off Oregon. Journal of the Fisheries Research Board of Canada 23(8): 1135-1143.
- PEQUEGNAT, W.E. & ROBERTS, T.W. 1971. Decapod shrimps of the family Penaeidae. In: Gulf of Mexico deep-sea fauna, Decapoda and Euphausiacea. Series Atlas of the marine Environment 20: 8-9.
- PÉREZ FARFANTE, J. 1973. Morphological study of diagnostic characters in Western Atlantic *Hepomachus* (Crustacea, Decapoda, Penaeidae). Fishery Bulletin, United States 69(3): 441-453.
1987. Revision of the gamba prawn genus *Pseudaristeus*, with description of two new species (Crustacea: Decapoda: Penaeoidea). Fishery Bulletin, United States 85(2): 311-338.
- PÉREZ FARFANTE, J. & KENSLEY, B.F. 1997. Penaeoid and sergestoid shrimps and prawns of the world. Keys and diagnoses for the families and genera. Mémoires du Muséum national d'Histoire naturelle 175: 1-233.
- RAMADAN, M.M. 1938. Crustacea: Penaeidae. John Murray Expedition 1933-34. Scientific Reports 5: 35-76.
- RATHBUN, M.J. 1906. The Brachyura and Macrura of the Hawaiian Islands. Bulletin of the U.S. Fisheries Commission 23:827-930.
- RISSO, A. 1816 Histoire naturelle des Crustacés des environs de Nice: 1-175 Paris.
- 1827 Histoire naturelle des principales productions de l'Europe Méridionale et particulièrement de celles des environs de Nice et des Alpes Maritimes, volume 5, vii + 403 pp (F.G. Levrault, Paris).
- ROBERTS, T.W. & PEQUEGNAT, W.E. 1970. Deep-water decapod shrimps of the family Penaeidae. In Pequegnat, W.E. & Chace, F.A. Jr (eds) Contributions on the Biology of the Gulf of Mexico. Texas A&M University Oceanographic Studies 1(3): 21-57.
- SENNA, A. 1903. Le esplorazioni abissali nel Mediterraneo del R. Piroscalo Washington nel 1881, II. Nota sui Crustacei Decapodi. Bollettino della Società Entomologica Italiana 34(4): 235-367.

- SMITH, S.I. 1882. Reports on the results of dredging, under the supervision of Alexander Agassiz, on the east coast of the United States, during the summer of 1880, by the U.S. Coast Survey Steamer "Blake", Commander J.R. Bartlett, U.S.N., commanding. *Bulletin of the Museum of comparative Zoology at Harvard College* 10(1): 1-108.
1884. Report on the decapod Crustacea of the Albatross dredgings off the east coast of the United States in 1883. *Annual Report of the Commissioner of Fish and Fisheries for 1882*: 345-424.
1886. the abyssal Decapod Crustacea of the Albatross dredgings in the North Atlantic. *Annals and Magazine of Natural History* (5)17: 187-198.
1887. Report on the decapod Crustacea of the Albatross dredgings off the east coast of the United States, during the summer and autumn of 1884, Report of the Commissioner of Fish and Fisheries 13: 605-706.
- SQUIRES, H.J. 1990. Decapod Crustacea of the Atlantic coast of Canada. *Canadian Bulletin of Fisheries and aquatic Sciences* 221: 1-532.
- STEBBING, T.R.R. 1914. South African Crustacea. (Part VII of S. A. Crustacea, for the Marine Investigations in South Africa). *Annals of the South African Museum* 15(1): 1-55.
- SUND, O. 1920. Peneides and stenopides from the "Michael Sars" North Atlantic Deep-Sea Expedition. Report of the Michael Sars North Atlantic Deep-Sea Expedition 3(2): 1-36.
- TIRMIZI, N.M. 1960. Crustacea: Penaeidae. Part II. Series Benthescymae. With a note by I. Gordon. *John Murray Exped. 1933-34, scient. Rep.* 10: 319-383.
- WASMER, R.A. 1972. New records for four deep-sea shrimps from the Northeastern Pacific. *Pacific Science* 26(3):259-263.
- WOOD-MASON, J. 1891. Phylum Appendiculata. Branch Arthropoda. Class Crustacea. *Annals and Magazine of Natural History* (series 6)8: 269-286.
1892. Illustrations of the zoology of the Royal Indian Marine Survey Steamer "Investigator". Crustacea, part 1, pls 1-5.
- WOOD-MASON, J. & ALCOCK, A. 1891a. Natural History Notes from H.M. Indian Marine Survey Steamer Investigator, Commander R.F. Hoskyn, R.N. commanding. No. 21. Note on the results of last season's deep-sea dredging. *Annals and Magazine of Natural History* (series 6)7: 186-202.
- 1891b. Natural History Notes from H.M. Indian Marine Survey Steamer Investigator, Commander R.F. Hoskyn, R.N. commanding. Ser. II, No. 1. On the results of deep-sea dredging during the season 1890-91. Phylum Appendiculata. *Annals and Magazine of Natural History* (series 6)8: 269-286.

FIRST RECORD OF THE LARGE-TOOTH COOKIE-CUTTER SHARK *ISISTIUS PLUTODUS* FROM AUSTRALIAN WATERS. *Memoirs of the Queensland Museum* 46(2): 442. 2001:- The largetooth cookiecutter shark *Isistius plutodus* Garrick & Springer (1964), is an epipelagic and possibly bathypelagic shark known only from the Gulf of Mexico, off Alabama, USA and the western North Pacific, off Okinawa, Japan (Compagno, 1984).

Isistius contains *I. plutodus* and *I. brasiliensis* (Quoy & Gaimard, 1824). Both species have small cigar-shaped bodies (maximum size about 42cm TL and 50cm TL respectively), a conical snout and two low, spineless dorsal fins. The most obvious differences between the two species are the number of tooth rows in the lower jaw and the distance between the two dorsal fins. In *I. plutodus*, there are 19 tooth rows in the lower jaw and the inter-dorsal distance is subequal to the base of the first dorsal fin (D1). In *I. brasiliensis* there are 25-31 tooth rows, and the inter-dorsal distance is over twice the D1 base (Compagno, 1984). A distinctive dark collar-like marking is found around the branchial region of *I. brasiliensis*.

A 363mm ♀ *I. plutodus* was recently identified in the Ichthyology Collection of the Australian Museum (AMS I.28924-001). The specimen was collected by the *FI Teresa* in 1988 off Newcastle, New South Wales (approximately 33°S 152°E). Full collection details are not available, but discussions with K. Bollinger, the vessel owner, indicate that the shark was probably caught at night as prawn bycatch in an otter trawl at a depth of about 100m.

The specimen has 19 tooth rows in the lower jaw and lacks a clearly defined collar around the branchial region. The snout is very short (14.2mm) and the eyes are anteriorly placed. Compagno (1984) suggested that the position of the largetooth cookiecutter's eyes allows for binocular vision, which aids in precisely locating its victims.

The AMS specimen of *I. plutodus* was fixed in formalin in 1988 and has been preserved since in 70% ethanol. The pectoral, anal and caudal fins are damaged and the tissue around the snout is distorted. This has affected accurate

measurement of several of the diagnostic characters, however all characters are consistent with the descriptions in Garrick & Springer (1964) and Compagno (1984). The specimen has the following morphometrics (in mm): TL 363, HL 68.6, snout length 14.2, eye length (including posterior notch) 15.0, predorsal length 233, body depth 36.7, D1 base 17.5, D1 height 10.6, D2 base 18.2, D2 height 13.2, interdorsal space 22.5, D2 insertion to upper caudal origin 26.2.

This major range extension is a new record for Australia and the Southern Hemisphere. The continental shelf in the region of the collection locality is approximately 42km wide. The fish was captured approximately 24km landward of the shelf break (200m isobath). Species of *Isistius* are believed to move vertically in the water column from deeper waters. If this is the case then the current fish not only ascended from deep water but also traversed over 20km in shelf (< 200m) waters.

Acknowledgements

Dr J.D. Stevens (CSIRO Fisheries, Hobart) is acknowledged for confirming the identification and for advice on the manuscript. C. Bento photographed the fish, and S. Morris retrieved the specimen from the collection and did an initial examination. K. Bollinger and the crew of the *FI Teresa*, are thanked for capturing the fish and sending it to the Australian Museum.

References

- COMPAGNO, L.J.V. 1984. FAO species catalogue. Vol.4, Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part I - Hexanchiformes to Lamniformes: viii, 1-250. FAO Fisheries Synopsis 125: 1-249.
- LAST, P.R. & STEVENS, J.D. 1994. Sharks and rays of Australia. (CSIRO: Canberra).
- GARRICK, J.A.F. & SPRINGER, S. 1964. *Isistius plutodus*, a new squaloid shark from the Gulf of Mexico. *Copeia* 4: 678-682.

Mark A. McGrouther, Australian Museum, 6 College Street, Sydney, 2000; 12 April, 2000.



FIG. 1. *Isistius plutodus* (AMS I.28924-001).

A REVISION OF *PROCAMBRIDGEA* FORSTER & WILTON, (ARANEAE:
AMAUROBIOIDEA: STIPHIDIIDAE)

VALERIE TODD DAVIES AND CHRISTINE LAMBKIN

Davies, V.E. & Lambkin, C. 2001 06 30: A revision of *Procambidgea* Forster & Wilton, (Araneae: Amaurobioidea: Stiphidiidae). *Memoirs of the Queensland Museum* **46**(2): 443-459. Brisbane. ISSN 0079-8835.

Procambidgea rainbowi Forster & Wilton and *P. cavernicola* Forster & Wilton have been redescribed and 10 new species described. These are *P. grayi*, *kioloa*, *otwayensis*, *ourimbah*, *hunti*, *carral*, *monteithi*, *lamington*, *hilleri* and *montana*. The species have been collected from sites in SE Queensland, northern and eastern New South Wales and from the Otway Range in Victoria. Cladistic analysis shows that they form a monophyletic group and infers that *Procambidgea* is more closely related to the Stiphidiidae than any other group. □ *Procambidgea*, new species, Stiphidiidae, Amaurobioidea, cladistics.

Valerie E. Davies, Honorary Associate, Queensland Museum, PO Box 3300, South Brisbane 4101; Christine L. Lambkin, Department of Zoology & Entomology, University of Queensland, St Lucia 4072, Australia; Present address: CSIRO, Entomology, PO Box 1700, Canberra 2601, Australia; 28 March 2001.

Procambidgea, an Australian genus of cribellate spiders was described by Forster & Wilton (1973: 134) and placed in the Stiphidiidae along with several ecribellate spiders from New Zealand. Comprehensive descriptions of the type species, *P. rainbowi* and *P. cavernicola* were given. Examination of further Australian species has shown the importance of several characters which we illustrate for these two species.

Procambidgea is a small spider, seldom exceeding 5.0 in length; it has the nondescript pattern of most amaurobioids (Lehtinen, 1967: figs 42-67). Webs are often in the hollows of fallen logs in the form of a small suspended sheet, on the underside of which the spider sits. In the same way that *Stiphidion facetum* has been introduced to New Zealand from Australia, recently *Procambidgea* has been found in Auckland, New Zealand.

MATERIAL AND METHODS

Spiders from rainforest areas in SE Queensland, from cave and forest areas in New South Wales (NSW) and 4 mature specimens from the Otway Ranges in Victoria were examined. Most were collected in pitfall (PF) traps. Notation of spines follows Platnick & Shadab (1975). Illustrations were drawn with the aid of a camera lucida; the left male palp is illustrated. The epigyna appear to be very conservative and vary little between species thus there is an emphasis on ♂ characters and ♂♂ only are used in the Key. Cladistic methods are given under heading 'Relationships of *Procambidgea*'.

ABBREVIATIONS. Museums: AM, Australian Museum, Sydney; MNZ, Museum of New Zealand, Te Papa Tongarewa, Wellington; QM, Queensland Museum, Brisbane; WAM, Western Australian Museum, Perth.

Collectors: CH, C. Horseman; GBM, G.B. Monteith; MRG, M.R. Gray; RJR, R.J. Raven; SRM, S.R. Monteith; VED, V.E. Davies.

Location data: SF, State Forest; NP National Park.

Anatomical: AL, abdomen length; ALE, anterior lateral eyes; ALS, anterior lateral spinnerets; AME, anterior median eyes; APOPH, apophysis; AW, abdomen width; C, conductor; CB, cymbium; CAL, calamistrum; CH, cheliceral; CL, carapace length; CR, cribellum; CW, carapace width; E, embolic; EG, epigastric groove; EPIG, epigynal; ID, insemination duct; MAP, major ampullate spigots; mAP, minor ampullate spigot; MT, metatarsal; P, patellar; PCB, paracymbial; PCR, paracribellar spigots; PE, parembolic; PLE, posterior lateral eyes; PLS, posterior lateral spinnerets; PME, posterior median eyes; PMS, posterior median spinnerets; RTA, retrolateral tibial apophysis; T, tarsal; TRICH, trichobothria.

Abbreviations on illustrations are explained in the legends.

SYSTEMATICS

Procambidgea Forster & Wilton

Procambidgea gen. nov. Forster & Wilton, 1973: 134

TYPE SPECIES. *Procambridgea rainbowi* Forster & Wilton.

DIAGNOSIS. Three-clawed cribellate. Red-brown cephalothorax and legs, darker abdomen with lighter chevron pattern which is often faded or absent. AME smallest; from above posterior row of eyes straight to slightly procurved, anterior row recurved (Fig. 1A); from the front posterior row strongly procurved (Fig. 5I). Cheliceral promargin with 2 large teeth and 4-5 minute teeth; retromargin with 7 small contiguous teeth decreasing in size towards the base of the fang (Fig. 1B). Prolateral filamentous seta at base of fang longer than other setae. Labium slightly longer than wide; sternum slightly longer than wide, pointed posteriorly. Legs 1423, without feathery hairs; incomplete pre-distal fracture on tarsi (Raven, in prep.). Trochanters notched. Tarsal trichobothria in single row increasing in length distally, bothrium collariform; tarsal organ slit-like, broadening distally. Cribellum with two spinning fields in female, large broad colulus in male. Small epigynum with median longitudinal ridge, anterior gonopores. Male palp with oval tegulum; course of sperm duct showing clearly. Conductor, a membranous plate often partly sclerotised with distal folds around the spiniform embolus (Fig. 1F). Median apophysis reduced or absent. Cymbium with or without long post-alveolar extension; with or without bulge (paracymbium) on proximal retrolateral edge; if present bulge with or without processes. ALS largest with short conical terminal segment; two major ampullate spigots in female. PLS slender with longer terminal segment.

KEY TO ♂♂ *PROCAMBRIDGEA* SPP.

1. Palpal tibia with proximal spur (Fig. 5E). *monteithi*
Palpal tibia without proximal spur 2
2. Paracymbium without processes 3
Paracymbium with processes (Fig. 5O) 9
3. Median apophysis absent. 4
Median apophysis present (Fig. 1M) 5
4. RTA with small dorso-retrolateral branch (Fig. 4K) *carrai*
RTA without small dorso-retrolateral branch. *rainbowi*
5. Cymbial alveolus as short or shorter than post-alveolus.
Posterior RTA absent 6
Cymbial alveolus longer than post-alveolus. Posterior
RTA present (Fig. 3E) *otwayensis*
6. Conductor large and membranous 7
Conductor small, often partly sclerotised. 8
7. RTA with dorso-retrolateral branch. *cavernicola*
RTA without dorso-retrolateral branch. *huntii*

8. Alveolus: post-alveolus about equal. Sperm duct with open loop (Fig. 2K) *kioloa*
Alveolus: post-alveolus 1:3. Sperm duct with closed loop *grayi*
9. Paracymbium with retrolateral process only. Loop of sperm duct simple *ourimbah*
Paracymbium with retrolateral and ventral processes. Loop of sperm duct complex (Fig. 5O) 10
10. Embolic region about half length of tegulum. Sperm duct with transverse loop 11
Embolic region about quarter length of tegulum. Sperm duct with longitudinal loop *montana*
11. Ventral paracymbial process pointed. Loop of sperm duct closed *lamington*
Ventral paracymbial process small and blunt. Loop of sperm duct open *hillieri*

Procambridgea rainbowi Forster & Wilton (Figs 1A-I, 8A)

P. rainbowi Forster & Wilton, 1973:134, figs 403-406; Brignoli, 1981: 533 (catalogue).

MATERIALS. HOLOTYPE: ♀, rainforest, Jenolan, Blue Mountains, NSW, Australia, 33°30'S, 150°23'E, 18 July 1970, R.R. Forster (AMKS30617). ALLOTYPE: ♂, same data as holotype. (AMKS30616). OTHER MATERIAL: NSW. ♂, Mt Wilson, Cathedral of Ferns area, 33°30'S, 150°23'E, PF, 14 Aug. 1978, CH (AMKS1677); ♀, same locality, PF, 15 Feb. 1978, CH (AMKS1506); ♀, Mt Wilson, under log, 28 Oct. 1981, CH, D. Kent (AMKS8412); ♀, Mt Wilson, Cathedral of Ferns, under log in rainforest, 17 Apr. 1974, MRG (AMKS32777); 3 ♀, same locality, in sheet webs in logs, 26 June 1974, MRG (AMKS32778); ♀, 18km E Woodford, Blue Mtns NP, 33°44'S, 150°33'E, under log, 17 Apr. 1974, MRG (AMKS32776).

DIAGNOSIS. Cymbium with slight sclerotisation of posterior retrolateral edge; long cymbial extension; post alveolus is x 1.5 length of alveolus. Without median apophysis; large membranous conductor. ♂ palp with long femoral and tibial segments.

DESCRIPTION. See Forster & Wilton (1973:134-135) for description of ♀ holotype and ♂ allotype.

Female. CL 2.1 AL 2.0. Legs: I 8.5; II 7.1; III 6.3; IV 8.1. Epigynum (Fig. 1C-E) with anterior gonopores, simple median insemination ducts to spermathecae (Note: the anterior swellings on insemination ducts (Forster & Wilton fig. 406) were not observed). Females 3.3-5.3 long.

Male. CL 2.5 AL 2.3. Legs: I 12.8; II 10.2; III 9.0; IV 11.3. ♂ palp (Fig. 1F-I): embolus short, spiniform arising from distal tegulum; large conductor; no median apophysis, sperm duct with simple loop before entering embolus. Ratio of cymbial alveolus: post-alveolus is 1:1.5. RTA

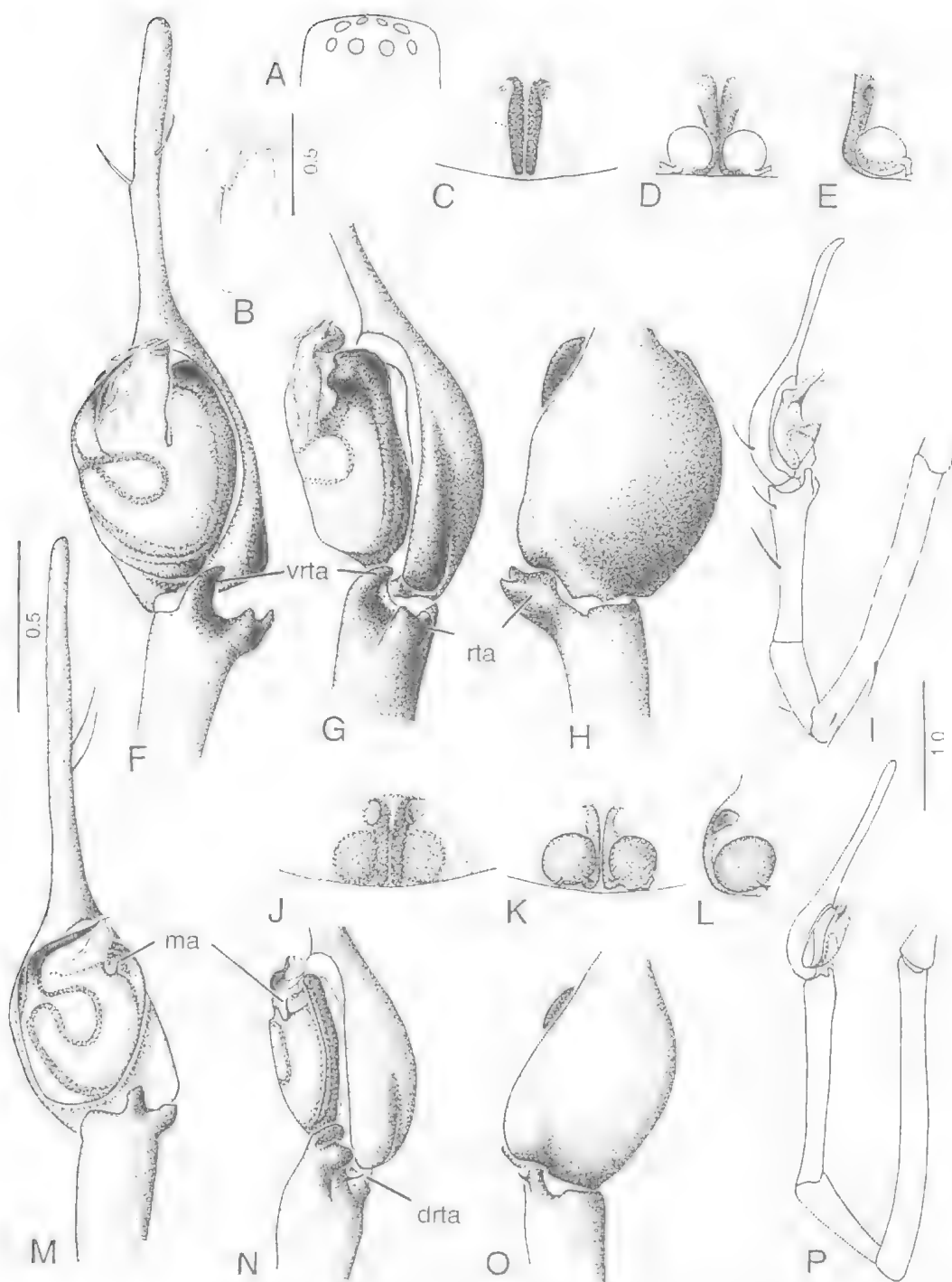


FIG. 1. A-I, *Procambridgea rainbowi* Forster & Wilton. A, eyes, dorsal; B, chelicera; C-E, epigynum (ventral, dorsal, lateral); F-I, ♂ palp (ventral, retrolateral, dorsal, entire palp). J-P, *Procambridgea cavernicola* Forster & Wilton: J-L, epigynum (ventral, dorsal, lateral); M-P, ♂ palp (ventral, retrolateral, dorsal, entire palp). drta = dorso-retrolateral branch of tibial apophysis; ma = median apophysis; rta = retrolateral apophysis; vrta = ventro-retrolateral branch of tibial apophysis.

with curved ventro-retrolateral and bifid retrolateral branches. Males 4.5-4.8 long.

DISTRIBUTION. Jenolan area, Blue Mountains, NSW (Fig. 8A).

***Procambidgea cavernicola* Forster & Wilton**
(Figs 1J-P, 8A)

P. cavernicola Forster & Wilton, 1973: 136, figs 407-410; Brignoli, 1981: 533 (catalogue).

MATERIAL. HOLOTYPE: ♂, Wee Jasper Signatore Cave, NSW, 35°09'S, 148°40'E, 2 June 1962, E. Hamilton-Smith (AMKS30614). ALLOTYPE: ♀, same data as holotype (AMKS30615). OTHER MATERIAL: NSW: 2♂, 3♀, Wee Jasper Punchbowl Cave Bat Chamber, 35°09'S, 148°40'E, 10 Sept. 1977, M. Marx (AMKS32758).

DIAGNOSIS. Cave species, less pigmented than *P. rainbowi*. Long cymbial post-alveolus twice length of alveolus; small slender median apophysis; RTA with extra needle-like dorso-retrolateral branch (cf., *P. rainbowi* in all these characters).

DESCRIPTION. See Forster & Wilton (1973: 136) for description of ♂ holotype and ♀ allotype.

Male. CL 2.3 AL 2.5. Legs: I 13.6; II 11.3; III 9.9; IV 12.5. ♂ palp (Fig. 1M-P) with small median apophysis. Cymbium with paracymbial bulge; ratio of alveolus: post-alveolus is 1:2.2. RTA with curved ventro-retrolateral, blunt retrolateral and a needle-like dorso-retrolateral branch. Sperm duct with simple open loop (i.e. arms of loop not touching). Males 4.5-4.8 long.

Female. CL 2.2 AL 3.1. Legs: I 10.5; II 9.3; III 8.2; IV 10.3. Epigynum (Fig. 1J-L) similar to *P. rainbowi* with slightly larger gonopores. [Note: The posterior process (Forster & Wilton fig. 409) is thought to be due to damage; it is not present on other females]. Females 5.3-5.5 long.

DISTRIBUTION. Wee Jasper, NSW (Fig. 8A).

***Procambidgea grayi* Davies sp. nov.**
(Figs 2A-G, 8A)

ETYMOLOGY. In honour of Michael Gray, arachnologist at the Australian Museum and collector of much of the material for this revision.

MATERIAL. HOLOTYPE: ♂, Lane Cove River Park nr Fullers Bridge, NSW, 33°47'S, 151°08'E, under rock Hawkesbury sandstone, 6 Apr. 1974, MRG (AMKS32770). PARATYPES: NSW. ♀, same data as holotype (AMKS58083); ♀, Gordon, 33°44'S, 151°09'E, PF, 24 Apr. 1984, CH (AMKS14400); ♀, Mooney Mooney Ck, 33°31'S, 151°12'E, in rainforest, 13 Jan.

1977, MRG (AMKS32771); ♂, ♀, Bobbin Head, Kuringai Chase NP, 33°39'S, 151°09'E in log, 10 Apr. 1974, MRG (AMKS32772); ♂, ♀, same data (AMKS32774); 2♀, same locality, sheet web under logs, 2 Nov. 1974, MRG (AMKS32773); ♂, ♀, St Ives, 33°44'S, 151°10'E, under log in wet sclerophyll forest, 7 Aug. 1971, MRG, G.E. Gray (AMKS32775). OTHER MATERIAL: **New Zealand.** ♀, ♂, juvs, Air Raid Tunnel, Alten Reserve, Auckland. NZMS 260 R11 685 820, 15 Oct. 1999, M. Hunt (MNZ).

DIAGNOSIS. ♂ palp with small membranous conductor with sclerotised tip (cf., *P. rainbowi*, *P. cavernicola*). Paracymbial bulge with small posterior projection. Needle-like median apophysis (cf., *P. rainbowi*).

DESCRIPTION. *Male.* CL 1.9 AL 2.1. ♂ palp (Fig. 2D-J) with short embolus; small membranous conductor; needle-like median apophysis. Simple sperm duct with arms of loop touching. Ratio of cymbial alveolus: post-alveolus is 1:1.3. Posterior edge of cymbium with small rounded projection. RTA with curved ventro-retrolateral and bifid retrolateral branches. Males 3.9-4.1 long.

Female. CL 2.2 AL 2.3. Epigynum (Fig. 2A-C) Females 3.3-4.6 long.

DISTRIBUTION. Sydney area, NSW (Fig. 8A) and introduced to Auckland, New Zealand.

***Procambidgea kioloa* Davies sp. nov.**
(Figs 2H-N, 8A)

ETYMOLOGY. From Kioloa SF, N.S.W.

MATERIAL. HOLOTYPE: ♂, Kioloa SF, Forest Drive, 16km N of Batemans Bay, NSW, 35°37'S, 150°16'E, PF, 28 June 1979, CH (AMKS3834). PARATYPES: NSW. 2♀, same locality and collector as holotype, 28 Aug. 1978, (AMKS1728); ♀, same locality and collector, 30 Apr. 1978 (AMKS1416); ♀, Boyne SF, Old Highway Rd, 35°38'S, 150°11'E, under rock, moist forest, 15 Aug. 1978, MRG (AMKS2074).

DIAGNOSIS. Posterior edge of cymbium with small projection (cf., *P. rainbowi*, *P. cavernicola*). Ratio of alveolus:post alveolus is 1:1 (cf., previous spp.). Sperm ducts with longitudinal loop with arms not touching (cf., *P. grayi*).

DESCRIPTION. *Male.* CL 1.8 AL 1.9. ♂ palp (Fig. 2K-N): very short distal embolus, small conductor, slender median apophysis. Arms of loop (longitudinal) in sperm ducts not touching. Cymbium with sclerotised posterolateral edge with small projection. Alveolus and post-alveolus about equal in length. RTA with

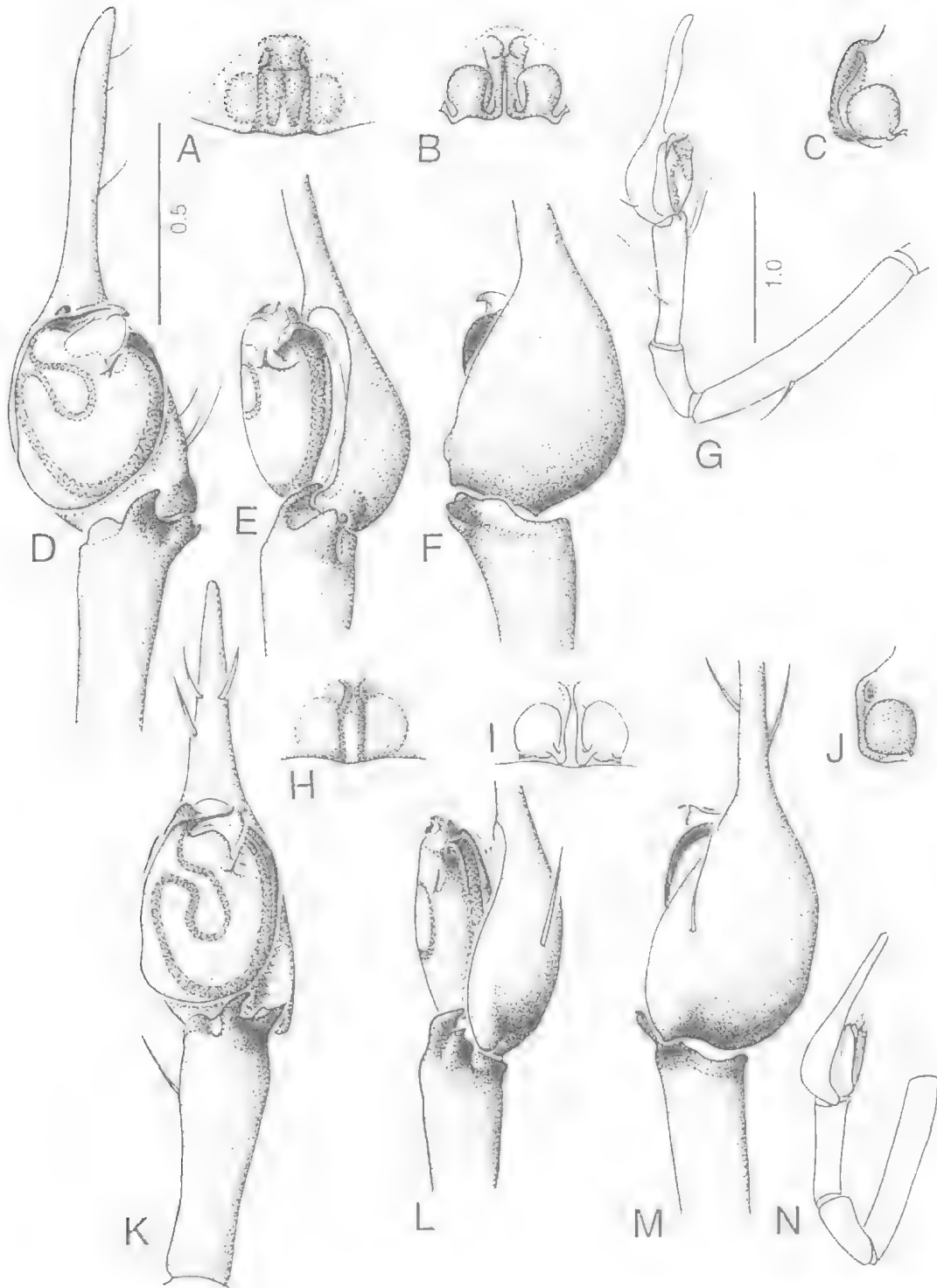


FIG. 2. A-G, *Procumbridgea grayi* sp. nov. A-C, epigynum (ventral, dorsal, lateral); D-G, ♂ palp (ventral, retrolateral, dorsal, entire palp). H-N, *Procumbridgea kioloa* sp. nov.; H-J, epigynum (ventral, dorsal, lateral); K-N, ♂ palp (ventral, retrolateral, dorsal, entire palp).

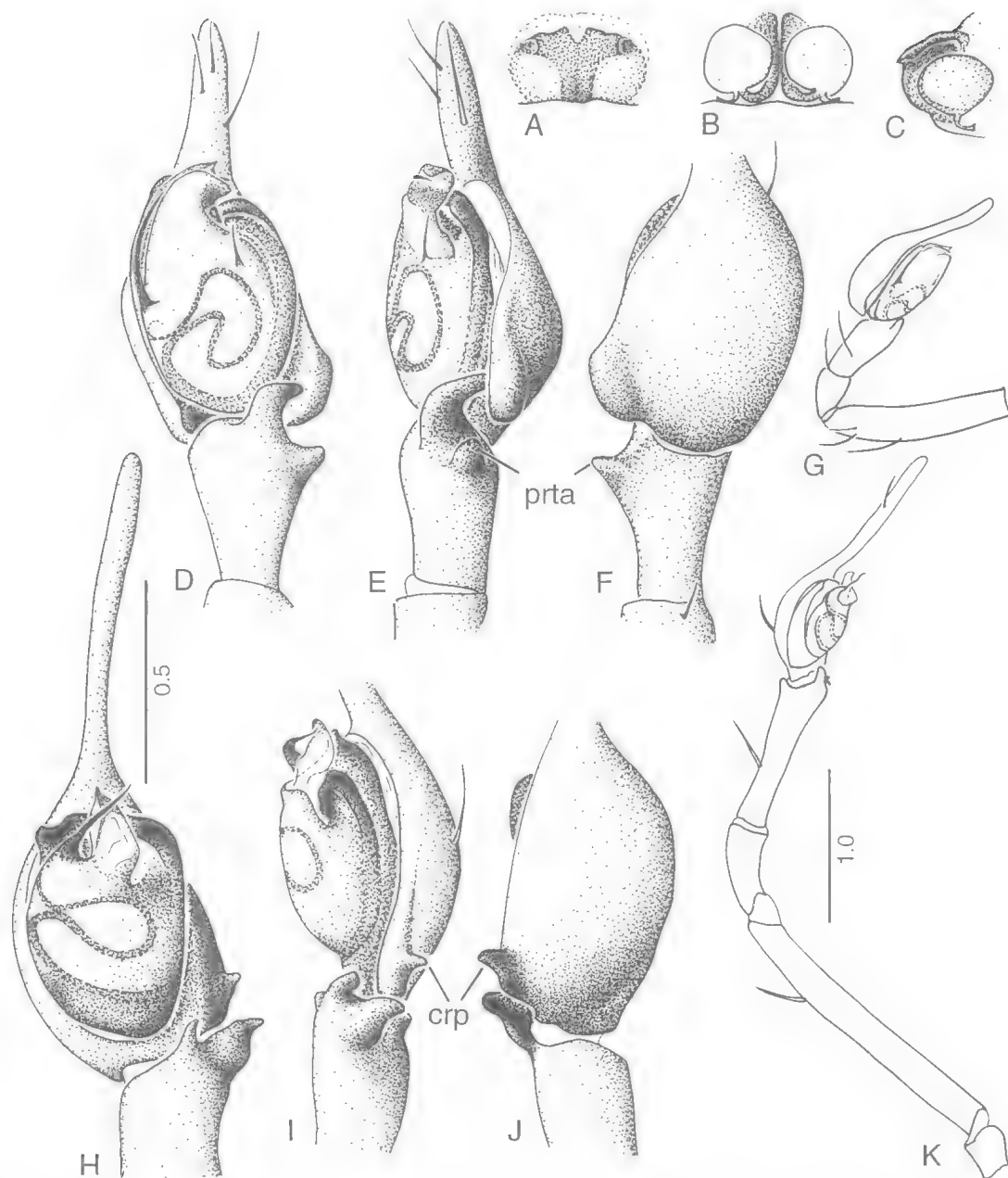


FIG. 3. A-G, *Procambridgea otwayensis* sp. nov. A-C, epigynum (ventral, dorsal, lateral); D-G, ♂ palp (ventral, retrolateral, dorsal, entire palp). H-K, *Procambridgea ourimbah* sp. nov. ♂ palp (ventral, retrolateral, dorsal, entire palp). crp = cymbial retrolateral process; prta = posterior retrolateral tibial apophysis.

ventro-retrolateral and pointed retrolateral branches.

Female. CL 1.9 AL 2.3. Epigynum (Fig. 2H-J). Females 3.3-4.5 long.

DISTRIBUTION. Kioloa SE, NSW (Fig. 8A).

***Procambridgea otwayensis* Davies sp. nov.**
(Figs 3A-G, 8A)

ETYMOLOGY. From Otway Range, Victoria.

MATERIAL. HOLOTYPE: ♂, Erskine Falls, Otway Ra., Victoria, 38°27'S, 143°58'E. in log beech eucalypt forest, 6

Apr. 1973, MRG (AMKS32764). Paratypes: Victoria, ♂, same data as holotype (AMKS58082); ♀, same locality, 5 Apr. 1973, MRG (AMKS32765); ♀, Beech forest, Otway Ra., 7 Apr. 1973, MRG (AMKS32766); ♀, Grey R. xing, Otways, 38°39'S, 143°50'E, 250m, 6 Nov. 1977, GBM, SRM (QMS42196).

DIAGNOSIS. Cymbial alveolus is twice as long as post-alveolus (cf., all previously described spp.). RTA with simple postero-retrolateral branch (cf., all described spp.).

DESCRIPTION. *Male.* CL 2.1 AL 2.2. Legs: I 11.4; II 9.7; III 8.0; IV 10.0. ♂ palp is short (Fig. 3D-G). Embolus spiniform arising from mid-prolateral tegulum; conductor large membranous; median apophysis needle-like. Course of sperm duct with arms of loop coming together and continuing parallel before the anterior arm enters embolus. Ratio of alveolus:post-alveolus is 1:0.5. Paracymbium a proximal bulge. RTA with ventro- and postero-retrolateral branches. Other ♂ was also 4.3 in length.

Female. CL 2.0 AL 2.3. Epigynum (Fig. 3A-C); gonopores open well lateral to the mid-line; spermathecae larger than other species. Females 4.1-4.3 long.

DISTRIBUTION. Otway Ra., Victoria (Fig. 8A).

***Procambridgea ourimbah* Davies sp. nov.**
(Figs 3H-K, 8A)

ETYMOLOGY. From Ourimbah, NSW.

MATERIAL. HOLOTYPE: ♂, Gosford-Ourimbah, NSW, 33°24'S, 151°21'E, under logs, rainforest, May 1993 (AMKS35169).

DIAGNOSIS. No median apophysis (cf., *P. cavernicola*, *P. gravi*, *P. kialoa*, *P. otwayensis*). Paracymbium with strong retrolateral process (cf., all previously described spp.).

DESCRIPTION. *Male.* CL 2.3 AL 1.9. ♂ palp (Fig. 3H-K) with small membranous conductor, sclerotised distally. No median apophysis. Sperm duct simple with closed loop. Paracymbium with retrolateral process. Ratio of cymbial alveolus:postalveolus is 1:1.4. RTA with small ventro-retrolateral and pointed retrolateral branches.

Female. (unknown).

DISTRIBUTION. Ourimbah, NSW (Fig. 8A).

***Procambridgea hunti* Davies sp. nov.**
(Figs 4A-F, 7, 8B)

ETYMOLOGY. In honour of the late Glenn Hunt, arachnologist and collector of the holotype.

MATERIAL. HOLOTYPE: ♂, Barrington Tops, NSW, 31°58'S, 151°28'E, eucalypt forest 1538m, 18 July 1971, G.S. Hunt (AMKS32761). Paratypes: NSW, 3 ♂, same data as holotype (AMKS58081); ♀, penult. ♂, Gloucester, 78km W of Barrington Tops Forest Rd, 32°01'S, 151°09'E, under log, 19 Mar. 1982, MRG; 11. Pamaby (AMKS8830); ♀, Tuglo, 50km NW Singleton, 32°14'S, 151°16'E, small sheet webs in logs, 19 Jan. 1977, MRG (AMKS32762).

DIAGNOSIS. A larger spider than other species. Very long post-alveolar region of cymbium, more than twice the length of alveolus (cf., all other spp. except *P. cavernicola*). RTA without small dorso-retrolateral branch (cf., *P. cavernicola*).

DESCRIPTION. *Male.* CL 2.8 AL 2.6. ♂ palp (Fig. 4C-F); embolus, slightly curved; conductor small with sclerotised tip; slender median apophysis; sperm duct with small open loop. Very long cymbium with sclerotised posterior edge; ratio of alveolus:post-alveolus is 1:2.4. RTA with ventro-retrolateral and bifid retrolateral branches. Males 5.2-5.8 long.

Female. CL 2.4 AL 2.5. Epigynum (Fig. 4A, B). The female from Tuglo was 7.2 long.

DISTRIBUTION. Eucalypt forest, Barrington Tops, NSW (Fig. 8B).

***Procambridgea carrai* Davies sp. nov.**
(Figs 4G-M, 7D, 8B)

ETYMOLOGY. From Carrai SE, N.S.W.

MATERIAL. HOLOTYPE: ♂, Carrai SE, NSW, 80km W of Kempsey 31°01'S, 152°20'E, rainforest, 18 July 1971, MRG; G.E. Gray (AMKS32747). **PARATYPES:** NSW, ♀, Carrai SE nr Carrai Bat Cave, in log, rainforest, 26 Apr. 1974, MRG (AMKS32748); 2 ♀, Carrai SE nr Carrai Arch Cave nr Kookaburra W of Kempsey, in cave, 1 Aug. 1971, L. Henshaw (AMKS32749); ♂, Carrai SE, start Kookaburra Trail, 31°02'S, 152°20'E, pyrethrum tree fern, 19 Oct. 1992, J. Stanisic, G. Ingram (QMS42240); 2 ♂, Mt Boss SE (Fenwicks), 31°12'S, 152°24'E, Oct. 1980, G.A. Webb, Forestry Commission (AMKS43510). **OTHER MATERIAL:** 2 ♂, Kerewong SE nr Lorne, 31°36'S, 152°34'E, PF, 15 July 1979, D. Milledge (AMKS5405); ♂, same data (AMKS5426); ♂, Kerewong SE, 31°35'S, 152°41'E, PF, 29 Aug. 1978, D. Milledge (AMKS1982).

DIAGNOSIS. RTA with dorso-retrolateral branch (cf., all species except *P. cavernicola*). Without median apophysis (cf., *P. cavernicola*).

DESCRIPTION. *Male.* CL 2.2 AL 2.3. ♂ palp (Figs 4J-M, 7D); short spiniform embolus, small conductor, without median apophysis. Sperm duct with open loop leading to embolus. Cymbium with sclerotised posterolateral edge; ratio of alveolus:post-alveolus is 1:1.8, RTA with

ventro-retrolateral, retrolateral and small dorso-retrolateral branches. Males 3.8-4.5 long. *Female*. CL 1.8 AL 2.1 Epigynum (Fig. 4G-I). Females 3.9-5.0 long.

DISTRIBUTION. Rainforest areas W of Kempsey, NSW, (Fig. 8B).

***Procambidgea monteithi* Davies sp. nov.**
(Figs 5A-G, 8B)

ETYMOLOGY. In honour of Geoffrey Monteith, collector *extraordinaire*.

MATERIAL. HOLOTYPE: ♂, Point Lookout, New England NP, NSW, 30°30'S, 152°24'E, 1300m, PF 101, *Nothofagus* forest, 11 Nov. 1980-16 Mar. 1981, GBM (QMS42206). PARATYPES: NSW. ♂ ♀, Point Lookout (upper), New England NP, 1400m, PF 100, 21 Mar-11 Nov. 1980, GBM (QMS42253).

DIAGNOSIS. Cymbial alveolus longer than post-alveolus (cf., all previously described species except *P. otwayensis*). No median apophysis (cf., *P. otwayensis*). Palpal tibia with proximal retrolateral spur (cf., all spp.).

DESCRIPTION. *Male*. CL 1.6 AL 1.3; ♂ palp (Fig. 5D-G) curved embolus; large membranous conductor, sclerotised retrolaterally; without median apophysis. Sperm duct with double loop. Cymbium with flange-shaped paracymbium without processes; cymbial alveolus longer than post-alveolus 1:0.6. RTA with ventro-retrolateral and non-bifid retrolateral branches. Tibia with proximal retrolateral spur. Other male larger, 3.8. *Female*. CL 1.7 AL 2.1. Epigynum (Fig. 5A-C) Gonopores widely separated; insemination ducts enter spermathecae medially.

DISTRIBUTION. In beech forest in New England NP, N NSW (Fig. 8B).

***Procambidgea lamington* Davies sp. nov.**
(Figs 5H-R, 8B)

ETYMOLOGY. From Lamington NP, Queensland.

MATERIAL. HOLOTYPE: ♂, Lamington NP, SE Queensland, 28°11'S, 153°11'E, 9-10 Aug. 1977, RJR (QMS42200). PARATYPES: Queensland. ♂, same data as holotype (QMS42239); ♀, 2♂, Lamington NP, notophyll forest, 9 July, 1977, RJR (QMS42199); ♀, Nagarigoon, Lamington NP, PF, 27 Mar-8 Apr. 1976, RJR, VED (QMS42201); 3♀, ♂, Nagarigoon Ck, 5 Apr. 1976, RJR, VED (QMS42215); ♂, Lamington NP, 9-10 Aug 1977, RJR (QMS42216); ♂, Binnaburra, Lamington NP, 1 July 1986, M.S. Harvey, P.J. Vaughan (WAM 98/2095); ♀, Daves Ck Country, Lamington NP, 3 Apr. 1976, RJR (QMS42217); ♀, Morans Falls, Lamington NP, 28°19'S, 153°05'E, 900m, Berlesate 924, rainforest stick

brushing, 15 Mar. 1997, GBM, B. Russell (QMS42218); ♀, Albert R, rt Branch, Lamington NP, 244m, PF 65, 8 Sept.-30 Oct. 1976, GBM, SRM (QMS42219). 5♂, 2♀, Springbrook, 28°15'S, 153°16'E, 1000m, rainforest, PF, 28 Oct. 1991, M. De Baar (QMS23032); 2♀, Springbrook Repeater Stn, 1000m, stick brushing Berlesate, 27 May 1997, GBM (QMS42198); ♀, Upper Tallebudgera Valley, SEQ. 28°14'S, 153°18'E, 530m. PF, Mar.-July, 1985, D. Cook (QMS42220); 2♂, 2♀, Mt Tamborine, 27°55'S, 153°10'E, 10 July 1974, VED, RJR, C.L. Wilton (QMS42254).

DIAGNOSIS. Paracymbium with retrolateral and ventral processes (cf. previously described spp).

DESCRIPTION. *Male*. CL 2.1 AL 2.0. ♂ palp (Fig. 5O-R); with curved embolus, large retrolaterally sclerotised conductor, no median apophysis; sperm duct with transverse double loop. Cymbial alveolus about twice as long as post-alveolus 1:0.6. Paracymbium with ventral and retrolateral processes. RTA with ventro-retrolateral and bifid retrolateral branches. Males 4.0-4.6 long.

Female. CL 2.0 AL 2.7. Carapace (Fig. 5H) without pattern. Sclerotisation of median epigynal ridge varies (Fig. 5J, K). Dorsal, lateral and posterior views (Fig. 5L-N) show the course of the insemination ducts. Females 3.6-4.7 long.

DISTRIBUTION. Lamington Plateau and Springbrook area, SE Queensland (Fig. 8B).

***Procambidgea hilleri* Davies sp. nov.**
(Figs 6A-G, 7A-C, 8B)

ETYMOLOGY. In honour of naturalist A. Hiller, collector of the holotype.

MATERIAL. HOLOTYPE: ♂, Mt Glorious, SE Queensland, 27°20'S, 152°46'E, rainforest, malaise trap, 27 June-18 Oct 1982, A. Hiller (QMS42203). PARATYPES: Queensland ♀, Mt Glorious NP, rainforest, 6 Jan. 1977, B.J. and M.J. Marples, RJR, VED (QMS42221); ♀, Mt Tenison Woods, 27°19'S, 152°44'E, 750m, rainforest, stick brushing, 15 May 1997, GBM (QMS42222); ♂, 22 Mar. 1979, GBM (QMS42255); ♂, Mt Mee, via Samford, 27°05'S, 152°41'E, 518m, rainforest, PF 14, 1974-1975, GBM, SRM (QMS42202); ♀, Mt Nebo, 27°23'S, 152°47'E, rainforest, 10 Sept. 1973, C. Wallace (QMS42256); 3♀, ♂, 2 penult. ♂, Booloumba Ck, Conondale Ra. SEQ, 26°39'S, 152°39'E, 13-18 May 1976, RJR (QMS42234); ♂, Casey Ck via Imbil, 26°29'S, 152°38'E, PF 3, 10 Aug.-9 Nov., 1974, GBM, SRM, (QMS42236); ♀, Mt Cabinet via Jimna, 26°43'S, 152°34'E, PF, 29 June-23 Aug. 1975, GBM, SRM (QMS42237); ♀ Tungi Ck, via Jimna, 26°39'S, 152°28'E, 550m, PF 28, 29 Mar.-16 June 1975, GBM, SRM (QMS42238).

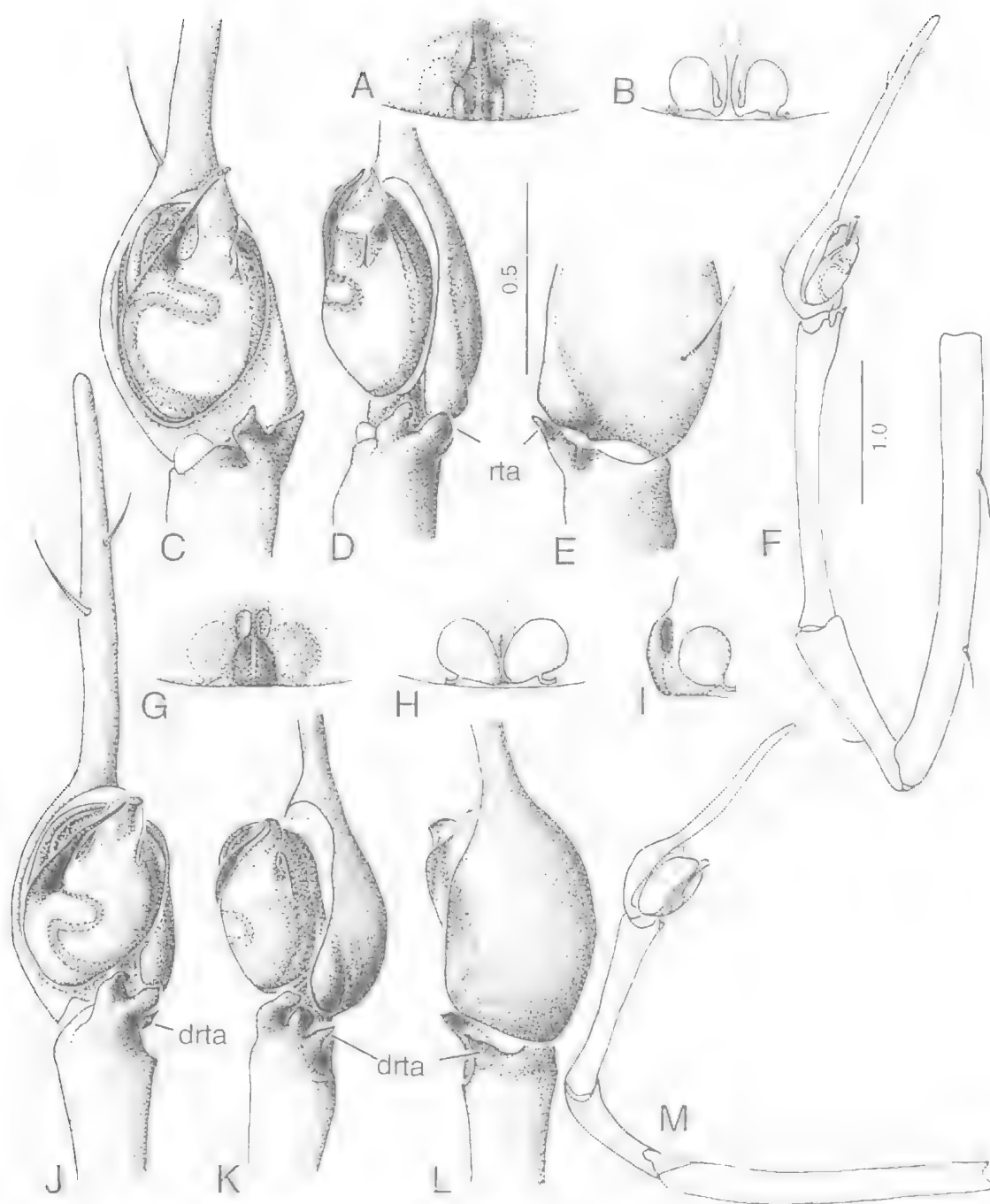


FIG. 4. A-F, *Procambridgea huntii* sp. nov. A, B, epigynum (ventral, dorsal); C-F, ♂ palp (ventral, retrolateral, dorsal, entire palp). G-M, *Procambridgea carrai* sp. nov.: G-I, epigynum (ventral, dorsal, lateral); J-M, ♂ palp (ventral, retrolateral, dorsal, entire palp). drta = dorso-retrolateral tibial apophysis; rta = retrolateral tibial apophysis.

DIAGNOSIS. Paracymbium with retrolateral *lamington*); ventral process small and blunt (cf., and ventral processes (cf., all species except *P. P. lamington* well-defined, pointed).

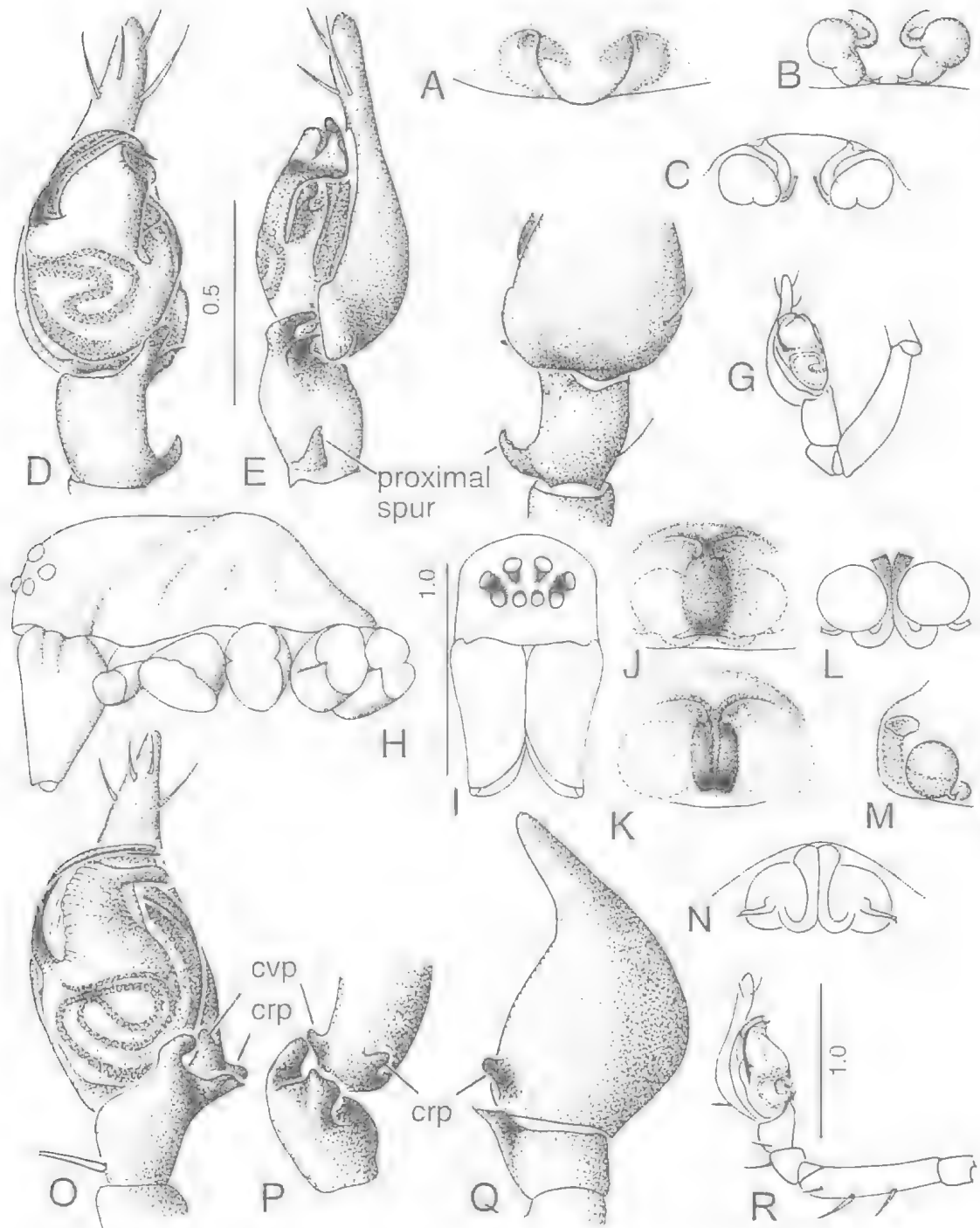


FIG. 5. A-G, *Procambbridgea monteithi* sp. nov. A-C, epigynum (ventral, dorsal, posterior); D-G, ♂ palp (ventral, retrolateral, dorsal, entire palp). H-R, *Procambbridgea lumingtoni* sp. nov.; H, carapace; I, Eyes, frontal; J, K, epigyna, ventral; L-N, epigynum (dorsal, lateral, posterior); O-R, ♂ palp (ventral, retrolateral, dorsal, entire palp). crp = cymbial retrolateral process; cyp = cymbial ventral process.

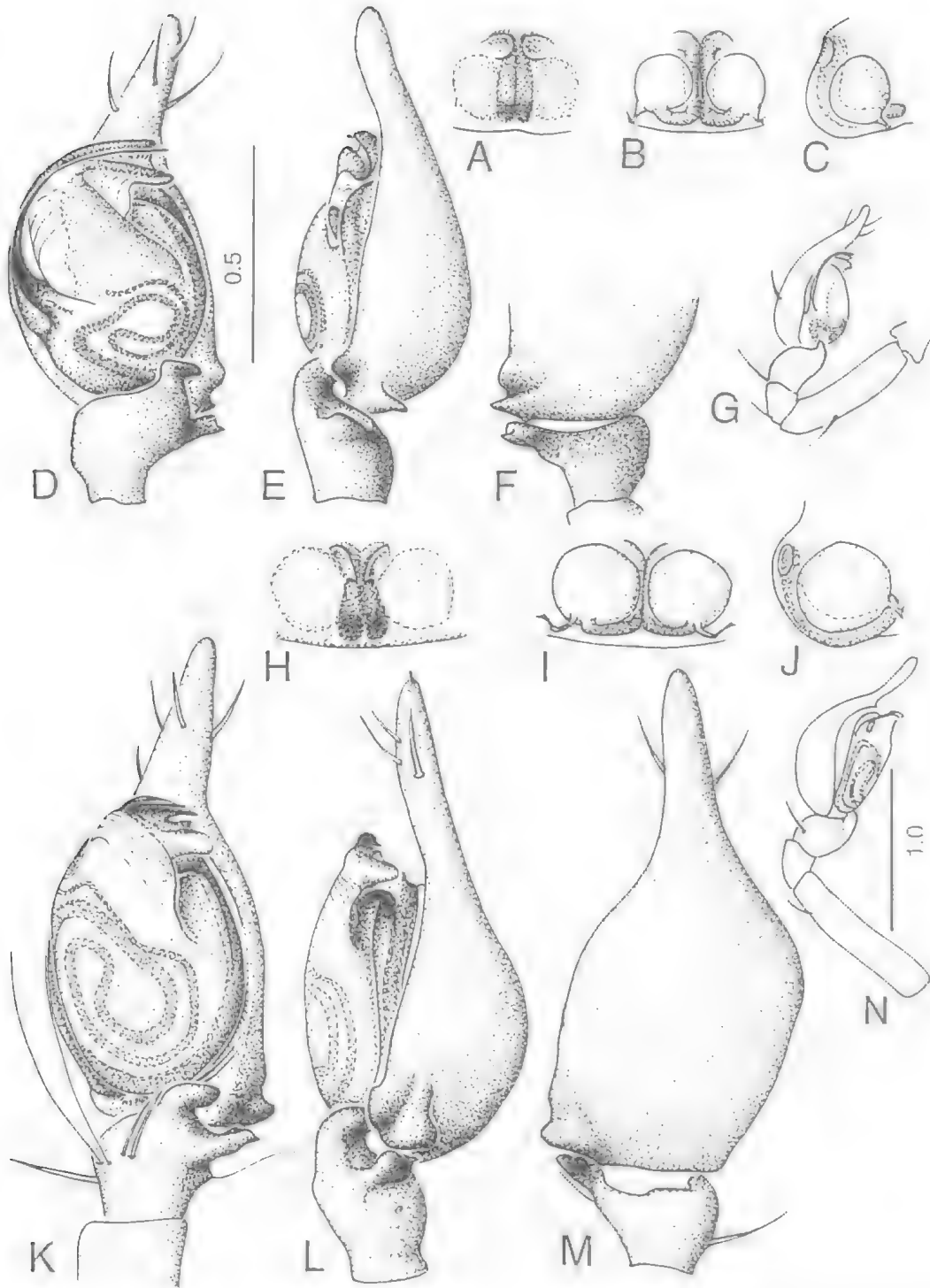


FIG. 6. A-G, *Procambridgea hilleri* sp. nov. A-C, epigynum (ventral, dorsal, lateral); D-G, ♂ palp (ventral, retrolateral, dorsal, entire palp). H-N, *Procambridgea montana* sp. nov.; H-J, epigynum (ventral, dorsal, lateral); K-N, ♂ palp (ventral, retrolateral, dorsal, entire palp).



FIG. 7. A-C, *Procambidgea hilleri* sp. nov.: A, epigynum; B, PMS(l.) with large mAP and PCR with 2 shafts; C, ♂ palp (ventro-retrolateral). D, *Procambridgen carrai* sp. nov. ♂ palp (ventral).

DESCRIPTION. *Male.* CL 1.9 AL 1.7. ♂ palp (Figs 6D-G, 7C) with large retrolaterally sclerotised conductor, no median apophysis; sperm duct with transverse double loop, arms of loop not touching. Cymbial alveolus: post-alveolus, 1:0.7. Paracymbium with sharp retrolateral spur and small blunt ventral process. RTA with obliquely angled ventro-retrolateral and bifid retrolateral branches. Males varied in length from 3.4-4.0.

Female. CL 1.8 AL 2.3. Epigynum (Figs 6A-C, 7A). ALS with 2 MAP, about 25 piriform spigots. PMS with large anterior mAP, some paracribellar spigots, one with 2 shafts on base (Fig. 7B), one posterior cylindrical spigot and aciniforms. Females 3.5-4.3 long.

DISTRIBUTION. D'Aguilar and Conondale Ranges, SE Queensland (Fig. 8B).

***Procambidgea montana* Davies sp. nov.**
(Figs 6H-N, 8B)

ETYMOLOGY. From Latin 'montanus', of mountains.

MATERIAL. **HOLOTYPE:** ♂, Mistake Mtns (north) 27°58'S, 152°22'E, via Goomburra, SE Queensland, 975m, PF 74, 13 Feb.-13 Oct. 1977, GBM, SRM (QMS42224). **PARATYPES:** Queensland. ♂, Mistake Mtns (middle) 27°58'S, 152°23'E, via Goomburra, 950m, PF 75, 13 Feb.-13 Oct. 1977, GBM, SRM (QMS42223); 2♀, Mistake Mtns, 16 Oct. 1976, RJR (QMS42226); ♂, Bald Mt via Emu Vale, 28°14'S, 152°22'E, 1130m, PF 20, 30 Mar.-2 Aug 1975, GBM, SRM (QMS42205); 3♀, Mt Superbus, 28°14'S, 152°28'E, PF, 12 Mar.-13 June 1990,

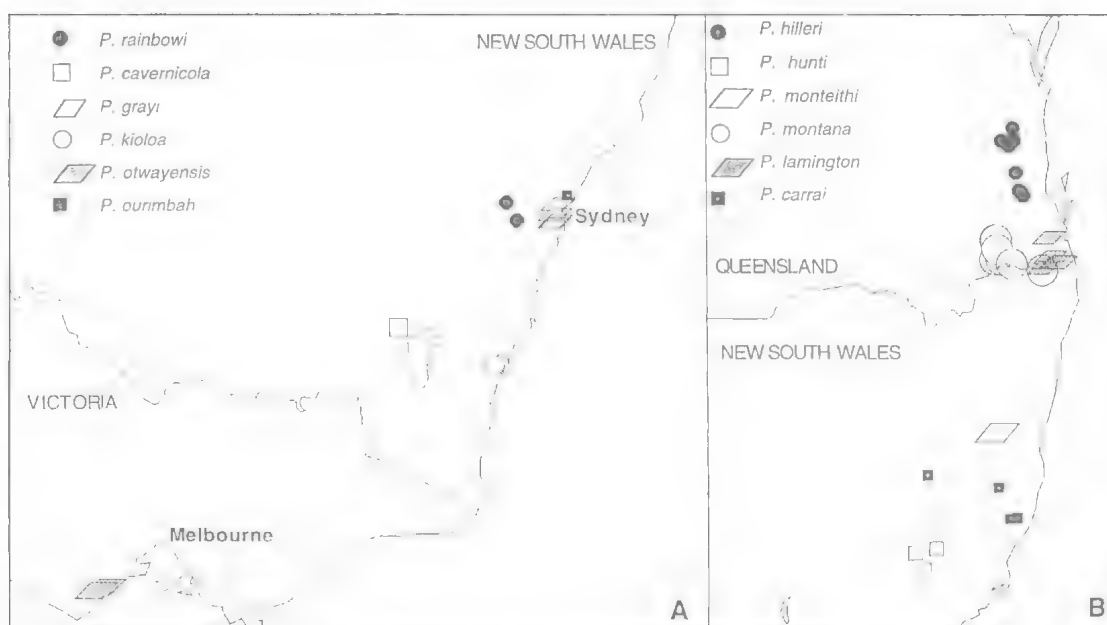


FIG. 8. A, B, Maps showing distribution of *Procambridgea* spp.

T. Churchill, RJR (QMS15917); ♀, Mt Superbus, 30 Oct. 1990, T. Churchill, RJR, K. Williams (QMS25888); ♂, ♀, same locality and collectors, 1000m, PF, 13 June–30 Oct. 1990 (QMS26292); ♀ Mt Superbus, 1360m, moss on tree trunks, 3 Mar. 1983, D. Yeates (QMS42258); stick brushing, GBM (QMS42259); ♀ Spicers Peak, 28°06'S, 152°24'E, 1200m, 30–31 Dec. 1993, GBM (QMS42230); ♂, 3♀, Cunninghams Gap, 28°03'S, 152°23'E, sieved litter, dry forest, 28 June 1991, D. Black (WAM 98/2084–7). NSW. 2♂, Nothofagus Mt via Woodenbong, 28°17'S, 152°37'E, 1100m, Berlesate No 416 from stick brushing, 17 June 1982, GBM, G. Thompson (QMS42197); ♂, ♀, Brindle Ck, Wangaree via Kyogle, 28°22'S, 153°04'E, 740m, PF 42, 22 Mar–2 Aug. 1975, GBM, SRM (QMS42257).

DIAGNOSIS. Short embolic area, about a quarter length of tegulum (cf., *P. hilleri*, *P. lamington*, about half length of tegulum). Sperm duct with longitudinal double loop (cf., *P. monteithi*, transverse double loop).

DESCRIPTION. *Male.* CL 1.8 AL 1.5. ♂ palp (Fig. 6K–N) with short distal embolus, membranous conductor, no median apophysis. Sperm duct in double loop (longitudinal rather than transverse). Ratio of alveolus: post-alveolus is 1:0.6. Paracymbium with very small ventral process and retrolateral process. Tibia short, as long as wide. RTA with curved ventro-retrolateral and bifid retrolateral branches. Males 3.2–3.8 long.

Female. CL 2.4 AL 2.4. Epigynum (Fig. 6H–J). Females 4.8–5.2 long.

DISTRIBUTION. In the area where the McPherson Range meets the Great Dividing Range (Fig. 8B) on the Queensland/New South Wales border.

RELATIONSHIPS OF *PROCAMBRIDGEA*

TERMINAL TAXA. A cladistic analysis examined 52 characters (Table 1) for relationships of the 12 *Procambridgea* spp. and 27 other Australian taxa as well as *Amaurobius* from the Northern Hemisphere, and *Amphinecta* and *Matachia* from New Zealand (Table 2). Outgroup comparison was with *Oecobius navus* Blackwall. The data matrix (Table 2) was prepared using MacClade version 3.08 (Maddison & Maddison 1999) and PAUP*. Fig. 9 was prepared using PAUP*. Fig. 10 was prepared using CLADOS version 1.2 (Nixon 1992) with DELTRAN optimisation.

DATA ANALYSIS. We analysed the data matrix for the 42 taxa (Table 2) using PAUP* version 4.0b4a (Swofford, 1999) on a Power Macintosh 7100/66. Heuristic searches of the data were completed using 10 random step-wise addition sequences, tree-bisection-reconnection (TBR) branch swapping, MULPARS, and branches having maximum length zero collapsed to yield polytomies. Strict and semistrict (Bremer, 1990) consensus trees of the most parsimonious trees (MPTs) were computed using PAUP*. Analyses

TABLE 1. Characters and character states.

1	AME: as large or larger than ALE (0); smaller (1)
2	CH: normal (0); small (1)
3*	Retromarginal CH teeth: no teeth (0); 1 (1); 2 (2); 3 (3); 3+ (4); 5+ (5)
4*	Promarginal CH teeth: no teeth (0); 2 (1); 3 (2); 3+ (3); 5+ (4)
5	Long prolateral seta at base of fang: absent (0); present (1)
6	Carapace: round (0); oval (1)
7	Enlarged frontal CH seta: absent (0); present (1)
8	Foveal area highest: absent (0); present (1)
9	♀ leg I: shorter than leg IV (0); equal to or longer than leg IV (1)
10	Stridulatory ridges on ♂ coxa I: absent (0); present (1)
11	Enlarged ventral spines on tibia and MT I and II: absent (0); present (1)
12	Feathery hairs: absent (0); present (1)
13	MT preening comb: absent (0); present (1)
14	MT TRICH: 2+ (0); 1 (1)
15*	T TRICH: 0 (0); 2+ (1); double row (2)
16	T rod: absent (0); present (1)
17	Anal tubercle: normal (0); enlarged (1)
18	CR spinning fields: 2 (0); 1 (1); absent (2)
19*	CAL: proximal (0); proximo-medial (1); long medial (2); no CAL (3)
20	MAP ♀ ALS: 2 (0); 1 and nubbin (1); 1 (2)
21	MAP ♀ ALS: mesal (0); anterior (1)
22*	PCR ♀ PMS: one shaft per base (0); more than one shaft (1); absent (2); no CR (3)
<i>Female characters</i>	
23	Medial EPIG atrium: absent (0); present (1)
24*	Posterior rim of medial atrium/EG: no medial atrium (0); close (1); well forward (2)
25*	ID: simple (0); loosely coiled (1); tightly coiled (2)
26*	Posterior EPIG scape: no scape (0); small knob (1); short (2); long (3)
27	Lateral projections on EPIG: absent (0); present (1)
28	Lateral EPIG teeth: absent (0); present (1)
<i>Male characters</i>	
29	E shape: spiniform (0); broad (1)
30	Direction of E: clockwise (0); anti-clockwise (1)
31	PE APOPH: absent (0); unbranched (1); branched (2)
32	E APOPH with 2-3 long setae: absent (0); present (1)
33*	E APOPH plate-like setae: absent (0); small (1); large (2)
34*	Shape of C: irregular (0); rounded (1); plate-like (2); T-shaped (3); s-shaped - falciform (4)
35	C/E: opposite (0); embracing (1)
36	Position of embracing C: retrolateral (0); prolateral (1)
37*	C length/tegulum: quarter (0); half (1); whole (2)
38	Secondary C: absent (0); present (1)
39	Median APOPH: absent (0); present (1)
40*	Loops of sperm duct: simple (0); 1 (1); 2 (2); 3 (3)
41	Orientation of CB to bulb: dorsal (0); mesal (1)
42*	CB alveolus/post-alveolus: shorter (0); equal (1); longer (2); twice as long (3)
43*	PCB process: absent (1); 1, retrolateral (1); 2, retrolateral and ventral (2)
44	RTA: absent (0); present (1)
45*	RTA/CB length: absent (0); quarter or less (1); more than half (2)
46	RTA dorsal branch: no RTA (0); branch absent (1); branch present (2)
47*	RTA with small dorso-retrolateral branch: no RTA (0); branch absent (1); branch present (2)
48	RTA extra distal branch: no RTA (0); extra branch absent (1); extra branch present (2)
49*	RTA proximal projection: no RTA (0); no proximal projection (1); proximal projection (2)
50	Tibial proximal retrolateral projection: absent (0); present (1)
51	Palpal tibia length/width: shorter to slightly longer than wide (0); much longer than wide (1)
52	Palpal P APOPH: absent (0); present (1)
[* Multistate characters treated as unordered]	

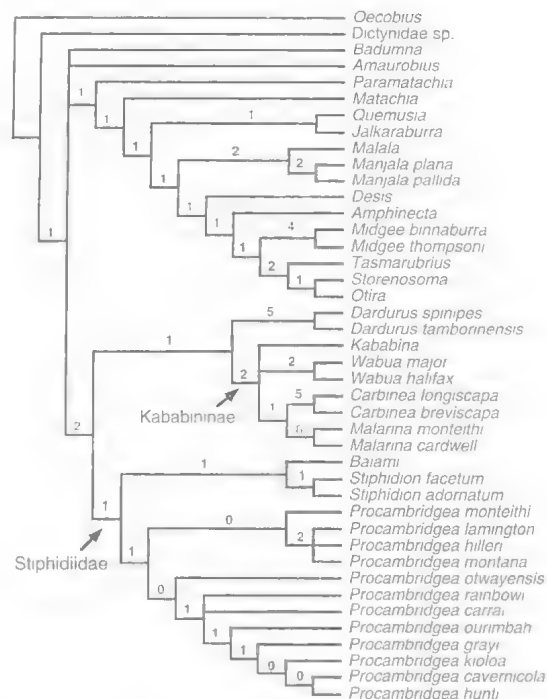


FIG. 9. Semistrict consensus of 36 MPT showing Bremer supports above the nodes.

were repeated using Hennig86 version 1.5 (Farris, 1988). The command mh* was used to find initial trees. The trees retained were then passed to the extended branch swapper, bb*. Bremer support (Källersjö et al., 1992) to indicate character support for nodes on the cladogram was calculated using the computer program TreeRot (Sorenson, 1999) on the preferred MPT with 20 random step-wise addition sequences, and support indicated above the nodes on the semistrict consensus tree (Fig. 9).

RESULTS. Heuristic searches of the 52 characters for the 42 taxa generated 36 MPTs of tree length 185, consistency index (Kluge & Farris, 1969) 0.46, consistency index excluding uninformative characters 0.42, retention index (Farris, 1989) 0.71 and rescaled consistency index 0.33. Hennig86 finds the same 36 MPTs. Many of the MPTs have terminal polytomies in *Procambidgea* (Fig. 10) as synapomorphic characters were not able to be scored across all taxa. Thus the strict consensus is less resolved. The MPTs are divided into two groups of 18 cladograms that differ markedly in the placement of *Amaurobius* in the Amaurobioidea (see

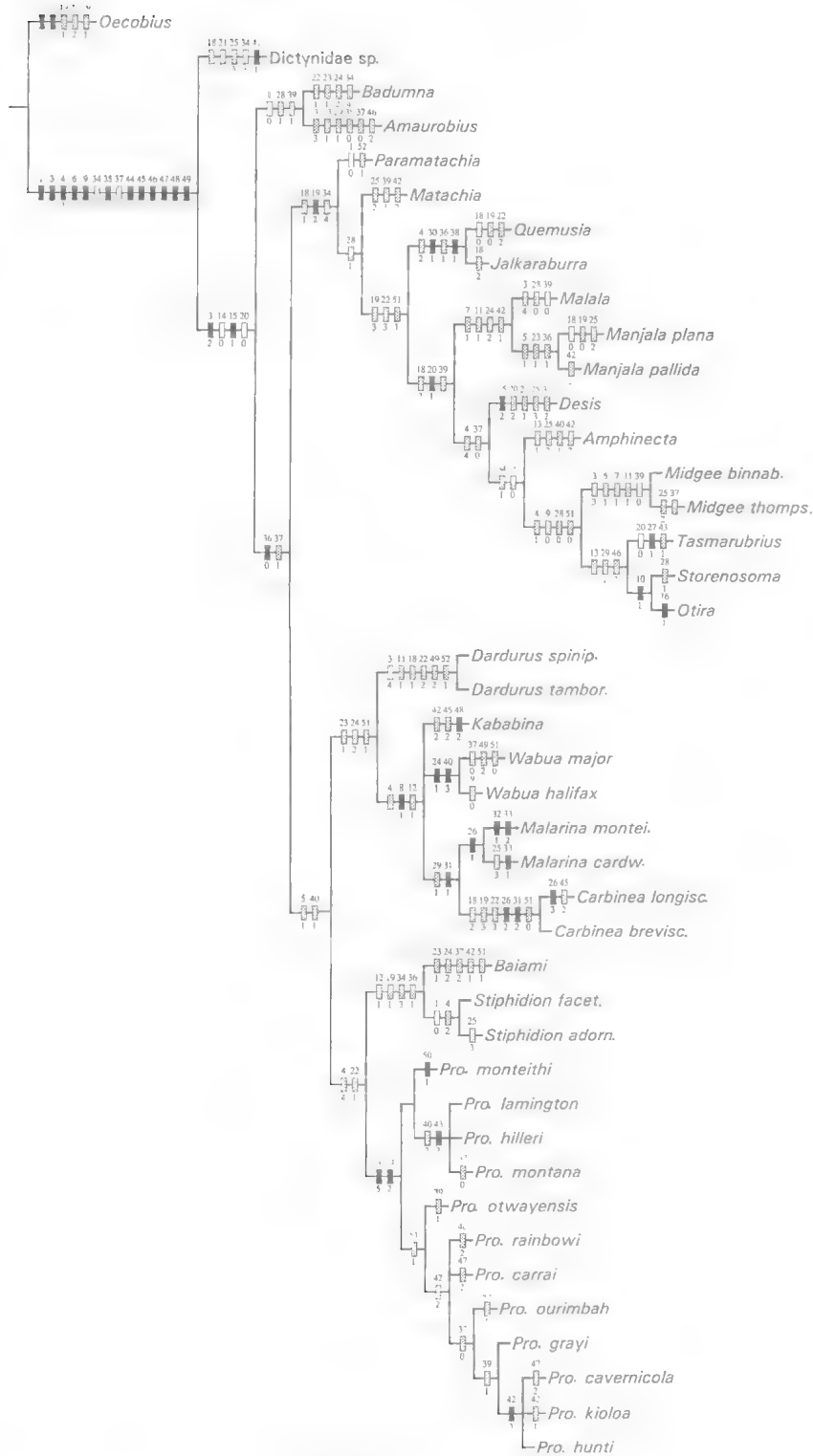


FIG. 10. Preferred most parsimonious tree showing characters and characters states.

TABLE 2. Data matrix.

Taxa	Character Number			
	10	20	30	50
<i>Cecobius navus</i> Blackwall	10000000	00000000	00000000	00000000
Dictynidae sp.	1013010010	0001000103	1000300000	0003112000
<i>Badumna longinqua</i> (Koch)	0023010010	0000100000	0112100100	0004112010
<i>Matachia ramulicola</i> Dalmas	1023010010	0000100120	0000200100	0004101017
<i>Paramatichia decorata</i> Dalmas	1024010010	0000200230	1300300100	0004102010
<i>Dasis</i> sp.	1024010010	0000200230	1300300100	0004102010
<i>Quemisia aquilonia</i> Davies	1022010010	0000100000	0200100101	0004111100
<i>Jalkaraburra alta</i> Davies	1022010010	0000100230	0300100101	0004111100
<i>Amphinecta milina</i> Forster & Wilton	1024010010	0010100231	0300200100	0001070011
<i>Amaurobius fenestralis</i> (Stroem)	1021010001	0010100231	0300100110	0001070010
<i>Storinosoma texanum</i> Davies	1021010001	0010100231	0300100110	0001070010
<i>Ohira summa</i> Davies	1021010001	0010100231	0300100110	0001070010
<i>Tasmarubius milvinae</i> (Simon)	1021010001	0010100230	0300100110	0001070010
<i>Stiphidion facetum</i> Simon	0022110010	0100100010	0100100000	0001111001
<i>Stiphidion adarnatum</i> Davies	0022110010	0100100010	0100100000	0001111001
<i>Baiaia volucris</i> (Simon)	1024110010	0100100010	0112100000	0003112000
<i>Midgee binraburra</i> Davies	1031111000	1000100311	0300100000	0001070010
<i>Midgee thompsoni</i> Davies	1031111000	1000100311	0300100000	0001070010
<i>Manjala plana</i> Davies	1023111010	1000100001	0312300100	0004111010
<i>Manjala pallida</i> Davies	1023111010	1000100231	0312300100	0004111010
<i>Malala lubinae</i> Davies	1043011010	1000100231	0302100000	0004101000
<i>Dardurus spinipes</i> Davies	1043110010	1000100100	0212100000	0001101001
<i>Dardurus tamborinensis</i> Davies	1043110010	1000100100	0212100000	0001101001
<i>Kababina alta</i> Davies	1021110110	0100100000	0312100000	0001101001
<i>Carbinea longiscapa</i> Davies	1021110110	0100100230	0312100010	2001101001
<i>Carbinea brevicauda</i> Davies	1021110110	0100100230	0312100010	2001101001
<i>Malarina monteithi</i> Davies	1021110110	0100100000	0012110010	1121101001
<i>Malarina cardwelli</i> Davies	1021110110	0100100000	0012310010	1011101001
<i>Wabua major</i> Davies	1031111010	0100100000	0011100000	0001100003
<i>Wabua halifax</i> Davies	1021110100	0100100000	0011100000	0001101003
<i>Procambidgea rainbowi</i> (Forster & Wilton)	1054110010	0000100000	0100100000	0003101002
<i>Procambidgea cavernicola</i> (Forster & Wilton)	1054110010	0000100000	0100100000	0003101002
<i>Procambidgea grayi</i> sp. nov.	1054110010	0000100000	0100100000	0003101002
<i>Procambidgea kioloa</i> sp. nov.	1054110010	0000100000	0100100000	0003101002
<i>Procambidgea otwayensis</i> sp. nov.	1054110010	0000100000	0100100000	0003101002
<i>Procambidgea outimbah</i> sp. nov.	1054110010	0000100000	0100100000	0003101002
<i>Procambidgea hanti</i> sp. nov.	1054110010	0000100000	0100100000	0003101002
<i>Procambidgea ceyrai</i> sp. nov.	1054110010	0000100000	0100100000	0003101002
<i>Procambidgea monteithi</i> sp. nov.	1054110010	0000100000	0100100000	0003101002
<i>Procambidgea lamington</i> sp. nov.	1054110010	0000100000	0100100000	0003101002
<i>Procambidgea hilleri</i> sp. nov.	1054110010	0000100000	0100100000	0003101002
<i>Procambidgea montana</i> sp. nov.	1054110010	0000100000	0100100000	0003101002

discussion). Thus the semistrict consensus of the 36 MPTs (Fig. 9) indicates a basal polytomy that leaves the placement of *Amaurobius* ambiguous. Nodes on the semistrict consensus tree (Fig. 9) that receive a Bremer support of 0 do not indicate conflict between the topologies but show that those nodes are unresolved in some of the MPTs. Figure 10 shows characters and character states on the preferred MPT with *Amaurobius* forming a basal clade with *Badumna*.

DISCUSSION

Cladistic analyses including many taxa of the Amaurobioidea, outlined the difficulty of family placement of the Kababininae (Davies, 1999; Davies & Lambkin, 2000, 2001). Analysis of the Amaurobioidea, including many taxa of *Procambidgea*, continues to present difficulties

with family placement. The Amaurobioidea, Kababininae, and *Procambidgea* form well-resolved clades. However, inclusion of *Procambidgea* with a further 12 taxa, into the analysis causes changes to the basal topology, and results in two alternative resolutions for the placement of *Amaurobius fenestralis* (Stroem). In 18 MPT *Amaurobius* forms a third, basal clade with *Badumna* (Fig. 10). Therefore in these MPTs the Amaurobioidea does not form the two distinct clades seen in previous analyses (Davies, 1999; Davies & Lambkin, 2000, 2001.). In the other 18 MPT *Amaurobius* is sister to the large clade including *Dardurus*, the Kababininae, *Stiphidion* and *Procambidgea*. In all MPT one clade continues to contain the type genera of the Desidae and Amphinectidae (Figs 9, 10).

Procambridgea forms a separate group, distinct from the Kababininae, and more closely related to *Stiphidion* and *Baiami*. The Bremer support for these relationships is poor, never more than 1, and based entirely on homoplasious characters (Fig. 10); thus *Procambridgea* remains in the Stiphidiidae. *Procambridgea* contains two species-groups: a northern group comprising *monteithi*, *lamington*, *hilleri*, and *montana* and a more southern group of *rainbowi*, *cavernicola*, *grayi*, *kioloa*, *ourimbah*, *hunti*, *carrai*, and *otwayensis*; however support for these groups is poor.

ACKNOWLEDGEMENTS

We are indebted to the curators and collection managers of the Australian, Western Australian and New Zealand Museums for loans of material and to all collectors of material for this revision. We thank the Council of the Australian Biological Resources Study for funding rainforest surveys in Queensland during which some of this material was collected and for financial support of illustrator and co-author, Christine Lambkin. She also set up the cladistic analyses resulting in the cladograms. We are grateful for the support of other members of the Queensland Museum, particularly Jennifer Cannon and Christine Thai for their help in the preparation of this paper.

LITERATURE CITED

- BREMER, K. 1990. Combinable component consensus. *Cladistics* 6: 369-372.
- BRIGNOLI, P.M. 1983. In Merrett, P. (ed.) *Catalogue of Araneae described between 1940-1981*. (Manchester University Press: Manchester, UK).
- DAVIES, V.T. 1999. A new spider genus from North Queensland, Australia (Araneae: Amaurobioidea: Kababininae). *Journal of Arachnology* 27 (1): 25-36.
- DAVIES, V.T. & LAMBKIN, C. L. 2000. *Malarina*, a new spider genus (Araneae: Amaurobioidea: Kababininae) from the wet tropics of Queensland, Australia. *Memoirs of the Queensland Museum* 45(2): 273-283.
2001. *Wabua*, a new spider genus (Araneae: Amaurobioidea: Kababininae) from north Queensland, Australia. *Memoirs of the Queensland Museum* 46(1): 231-249.
- FARRIS, J.S. 1988. Hennig86 Version 1.5. Port Jefferson: New York.
1989. The retention index and the rescaled consistency index. *Cladistics* 5: 417-419.
- FORSTER, R.R. & WILTON, C.L. 1973. The spiders of New Zealand. Pt IV. *Otago Museum Bulletin* 4: 1-309.
- KALLERSJÖ, M., FARRIS, J.S., KLUGE, A.G. & BULT, C. 1992. Skewness and permutation. *Cladistics* 8: 275-287.
- KLUGE, A.G. & FARRIS, J.S. 1969. Quantitative phyletics and the evolution of Anurans. *Systematic Zoology* 18: 1-32.
- LEHTINEN, P.T. 1967. Classification of the cribellate spiders and some allied families, with notes on the evolution of the suborder Araneomorpha. *Annales Zoologici Fennici* 4: 199-468.
- MADDISON, W.P. & MADDISON, D.R. 1999. *MacClade Version 3.08a*. (Sinauer Assoc. Inc.: Sunderland, Massachusetts).
- NIXON, K.C. 1992. *Clados, Version 1.2*. (L.H. Bailey Hortorium, Cornell University: Ithaca).
- PLATNICK, N.I. & SHADAB, M.U. 1975. A revision of the spider genus *Gnaphosa* (Araneae: Gnaphosidae) in America. *Bulletin of the American Museum of Natural History* 155: 1-16.
- SORENSEN, M.D. 1999. *TreeRot, Version 2*. (Boston University: Boston, Massachusetts).
- SWOFFORD, D.L. 1999. *Phylogenetic Analysis Using Parsimony (* and other methods). Version 4.0b4a*. (Sinauer Assoc. Inc.: Sunderland, Massachusetts).

SOUTHERN RANGE EXTENSION FOR THE DELICATE MOUSE (*PSEUDOMYS DELICATULUS*).

Memoirs of the Queensland Museum 46(2): 460, 2001.-Watts & Aslin (1981) described the delicate mouse (*Pseudomys delicatulus*) as a species of the tropical north, from Port Hedland in Western Australia to Bundaberg in Queensland. Despite being widespread, this small cryptic species is rarely encountered across much of its range (Watts & Aslin, 1981). In favourable habitat patches, *P. delicatulus* populations have been found to undergo dramatic fluctuations, sometimes producing brief eruptions after long periods of continuous breeding, later becoming uncommon (Braithwaite & Brady, 1993).

Increased biological survey activity in southeastern Queensland in the past decade has recognised a considerable southward extension of the known range for *P. delicatulus*. It was reported from Lake Broadwater Conservation Park 25km southwest of Dalby (27°20'S 151°00'E) in August 1996 (QM J11410) (Mathieson et al., 1999). This note reports a further southerly range extension of 130km for *P. delicatulus* to a site south of Inglewood following the capture of an individual during a larger project investigating the flow-on effects on biodiversity resulting from rabbit calicivirus disease induced declines in rabbit numbers.

The survey site is located on 'Whetstone' (28°31'S 150°55'E), 19km SW of Inglewood. The study site consists of three broad habitat types: 1) cracking clay soils adjacent to McIntyre Brook supporting a partially cleared woodland of forest red gum (*Eucalyptus tereticornis*), river red gum (*E. camaldulensis*) and rough-barked apple (*Angophora floribunda*) with an understorey of long grass (*Stipa* spp.); 2) alluvial plains, including an area of pasture, originally a poplar box (*E. populnea*) woodland, now grazed by cattle; and 3) a partially-cleared woodland of cypress pine (*Callitris glaucochrylla*), *Eucalyptus* spp. and bullock (*Allocasuarina luehmannii*) on sandy-textured solodic soils, adjacent to an extensive State Forest.

Small vertebrate faunas were surveyed at 8 sites using 4 Elliott trap formations and 4 pitfall lines. There was 1 trap site of each type in the two woodland communities; one along the river and another adjacent to the State Forest. The remaining 4 sites were located within the pasture habitat, which made up a substantial part of the site. Each Elliott trap site consisted of 49 traps arranged in two cross-arms. Elliott traps were spaced at 10m intervals and baited with a mixture of peanut butter and rolled oats. Pitfall trap sites consisted of a continuous 32m aluminium fly-wire drift fence positioned over 7 evenly spaced pits (PVC pipe 15cm diameter, 50cm deep) buried flush with the ground. Trapping was conducted for three consecutive nights.

Whetstone was trapped on nine occasions between October 1996 and June 1999, giving a total trapping effort of 5,145 Elliott trap nights and 588 pitfall nights. A single male *P. delicatulus* (QM J12786) was captured in an Elliott trap during May 1997 near the State Forest. The habitat surrounding the trap was mostly bullock regrowth on sandy soils with several large fallen trees providing considerable cover. No further *P. delicatulus* were captured despite this site

being sampled on six occasions between August 1997 and June 1999. Extra trapping conducted (100 Elliott trap nights) in bullock regrowth closer to the State Forest boundary in June 1999 and analysis of 70 fox/cat scats collected from the site in winter of 1997 and 1999 (Palmer unpubl. data) also failed to detect this species.

Mus domesticus was the most common and widespread mammal species captured. It was most common (33.3 mice per 100 Elliott trap nights) when the *P. delicatulus* was captured, but numbers were generally low at the site adjacent to the State Forest compared with other sites. Two other native species, *Sminthopsis murina* and *Antechinus flavipes*, were captured. These species were rare, but most individuals were trapped in similar habitat (bullock regrowth) to *P. delicatulus*. No native mammals were captured at the sites within the pasture.

The mouse was kept as a live specimen at the Queensland Museum for almost two years. Initially it was thought to be a Pilliga mouse (*P. pilligaensis*). Later examination of the mouse's skull revealed that it was a *P. delicatulus* or closest to this species. In the meantime, this individual was incorrectly reported by Sandell & Start (1999) to be a *P. pilligaensis*, as a result it appears in the Rabbit Calicivirus Disease Program Report 4' as this species.

This specimen and several others from SE Queensland and far N Queensland raise a number of taxonomic questions. Lack of a holotype for *P. delicatulus* and problems faced with obtaining topotype specimens may make the process of revising this species difficult (S. Van Dyck, pers. com.).

Acknowledgements

This work was part of a larger study of rabbit calicivirus funded by Land Protection Branch of the Queensland Department of Natural Resources. Thanks go to Steve Van Dyck for identifying the specimen. Technical support was provided by G. Story, D. Moore, W. Gould, A. Gonzalez and S. Pidcock.

Literature Cited

- BRAITHWAITE, R.W. & BRADY, P. 1993. The Delicate Mouse, *Pseudomys delicatulus*: a continuous breeder waiting for the good times. *Australian Mammalogy* 16: 93-96.
- MATHIESON, M., JOHNSON, R. & HOBSON, R. 1999. Additional vertebrate fauna records for Lake Broadwater Conservation Park. *Queensland Naturalist* 37: 1-3.
- SANDELL, P.R. & START, A.N. 1999. Rabbit Calicivirus Disease Program Report 4: Implications for Biodiversity. A report of research conducted by participants of the Rabbit Calicivirus Disease Monitoring and Surveillance Program and Epidemiology Research Program. (Bureau of Rural Sciences: Canberra).
- WATTS, C.H.S. & ASLIN, H.J. 1981. The rodents of Australia. (Angus and Robertson: Sydney).

R.A. Palmer, Department of Natural Resources, Robert Wicks Pest Animal Research Centre, PO Box 318, Toowoomba 4350; current address: Department of Zoology and Entomology, University of Queensland, St Lucia 4072; 7 August 2000.

THE FOSSIL RECORD OF *ELAEOCARPUS* L. FRUITS

MARY E. DETTMANN AND H. TREVOR CLIFFORD

Dettmann, M.E. & Clifford, H.T. 2000 06 30: The fossil record of *Elaeocarpus* L. fruits. *Memoirs of the Queensland Museum* 46(2): 461-497. Brisbane. ISSN 0079-8835.

Elaeocarpus L. fruit stones from Australian mid-Tertiary sediments are systematically described and their stratigraphic and geographic distributions recorded. The fossil fruit stones comprise 2-9-loculate inner mesocarps, their outer surface with longitudinal sutures and a sculpture ranging from smooth to pitted, baculate/verrucate/echinate/rugulate, or fossulate. The fertile locules have a near apical seed and the seedless locules are usually compressed; thin-walled endocarps dehiscence loculicidally and enclose the locules. The seed coat is bitegmic and has a multiplicative tegmen, the outer epidermis of which comprises thick-walled, pitted sclereids. Five types of fruit stones are distinguished on the basis of their surficial sculpture. Types 1 and 2 have verrucate/rugulate surfaces, Type 1 being distinguished by a higher ratio (>0.1) of sculptural base diameter:transverse diameter of fruit stone than that of (<0.1) Type 2 fruit stones. Types 3, 4, and 5 have pitted, smooth, and fossulate surfaces respectively.

A review of fossil fruit stones attributed to *Penteune* F.Muell., 1874, *Pleioclinis* F.Muell., 1882, *Phymatocaryon* F.Muell., 1871, and *Rhytidotherca* F.Muell., 1871 confirms these categories are congeneric with *Elaeocarpus*. One new species, *E. rozefeldsii*, is proposed and type specimens are designated for *E. allportii* (F.Muell.) comb. nov., *E. angularis* (F.Muell.) Selling, 1950, *E. bivalve* (F.Muell.) comb. nov., *E. brachyclinis* (F.Muell.) comb. nov., *E. couchmanii* (F.Muell.) comb. nov., *E. johnstonii* (F.Muell.) comb. nov. (and its junior synonym, *E. bassii* Ettingsh.), *E. lynchii* (F.Muell.) Selling, 1950, *E. muelleri* Ettingsh., 1886, *E. pleioclinis* (F.Muell.) comb. nov., and *E. trachyclinis* (F.Muell.) Selling, 1950.

The fossil fruit stone record confirms that *Elaeocarpus* was represented in the eastern Australian flora as early as the Early Oligocene. Modifications to the distribution range and diversity levels of the genus have occurred in eastern Australia since the Neogene. These involved the loss of taxa with Type 5 stones from Australia and a shift to more northerly areas of eastern Australia of species groups with Types 2, 3, and 4 fruit stones. □ *Elaeocarpus*, fossil fruit stones, Australia, mid-Tertiary.

Mary E. Dettmann, Department of Botany, The University of Queensland, St Lucia 4072; H. Trevor Clifford, Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; 8 November 2000.

Elaeocarpus L., a genus of ~ 60 or 360 species (Mabberley, 1987) occurring in tropical and warm regions of the Old World excluding Africa has an extensive fossil record from Tertiary sediments of eastern Australia. The fossil taxa are leaf remains that include compressions, impressions and cuticles (Ettingshausen, 1883; 1886; Christophel, 1994; Carpenter et al., 1994) and fruits that occur as permineralised casts and moulds or charcoalified compressions (Mueller, 1871a,b, 1873, 1874a,b, 1878, 1882; Johnston, 1880a,b, 1882; Ettingshausen 1883, 1886; Deane, 1925; Berry, 1926; Kirchheimer, 1935; Selling, 1950; Rozefelds, 1990; Rozefelds & Christophel, 1996a, b, in press; Burrows, 1997). *Elaeocarpus*-type pollen has been recorded extensively from eastern Australian sediments of late Eocene-Recent age (Luly et al., 1980; Truswell et al., 1987; Kershaw et al., 1994; Blackburn & Sluiter, 1994; Martin, 1998) but the

small, psilate, tricolporate pollen are difficult to discriminate from those of certain other Elaeocarpaceae (e.g. *Sloanea*) and Cunoniaceae, and detailed comparative studies on pollen of the two families are not available.

The present paper incorporates a taxonomic account of fossil *Elaeocarpus* fruit taxa reported from Australia, and documents their known geographic and stratigraphic distributions. Eighteen species of fossil fruits referable to *Elaeocarpus* have been reported from mid-Late Cainozoic sediments of eastern Australia, and one is newly described herein.

STUDIES ON FOSSIL FRUITS OF *ELAEOCARPUS*

In 1883 Ettingshausen described fossil fruits from Tasmania under the name *Elaeocarpus bassii* and was thus the first to attribute fossil fruits to the genus from the Australian Tertiary.

However, the earliest reference to fossil fruits consistent with those of *Elaeocarpus* dates from Mueller & Smyth's (1870:390) reference to a 'five valved capsule of an unknown genus' recovered from deep lead sediments at Haddon, Victoria. Specimens answering to that description were subsequently attributed to *Penteune*, which name is 'an allusion to the five valves in which the seeds are imbedded' (Mueller, 1874a: 41). Mueller is the author of 10 other fossil fruit species consistent with *Elaeocarpus* and instituted (1871a,b, 1874a, 1882) *Rhytidotheca*, *Phymatocaryon*, *Penteune* and *Pleioclinis*, to accommodate them. *Pleioclinis* was first used without a description or illustration in a note accompanying the description of *Rhytidotheca pleioclinis* (Mueller, 1873), and was formally described later (Mueller, 1882).

Mueller's generic diagnoses must be treated with caution for they do not always comply with the characters displayed by the species he attributed to them. For instance, *Penteune* was proposed for fruits with surface sculpture 'very slightly rough on the dorsal part' (Mueller, 1874a: 41), but on the same page, *P. trachyclinis*, is described as 'externally very rough, almost verrucular'. For *Pleioclinis* seed placentation was diagnosed as pendent (Mueller, 1882: 43), but in *Rhytidotheca pleioclinis* F. Muell., which was later transferred to *Pleioclinis* (Mueller, 1882), the seeds are said to be erect. Furthermore, fruit-valve number, a character that initially discriminated the genera, was later found to be variable; original diagnoses were not emended.

Mueller had difficulty in discriminating between his genera. For instance, he (Mueller, 1874b: 42) emphasised the sculptural similarity between the 5-valved *Penteune trachyclinis* and the 2-4 valved *Phymatocaryon mackayi*, but later (Mueller, 1875: 41) reported that fruits of *P. trachyclinis* with 4 valves bore much resemblance to *P. mackayi*. Subsequently, he (Mueller, 1882: 43) observed that *P. trachyclinis*

resembled rare 5-valved specimens of *Pleioclinis couchmanii*, the diagnosis of which specified 7-9, rarely 6 valves. It is also likely that Mueller had doubts that *Penteune* and *Rhytidotheca* were discrete genera as he noted for *Penteune clarkei* that 'some affinity of these fossils to those of the genus *Rhytidotheca* is evident' (Mueller, 1874b: 41). Thus, over 8 years Mueller directly or indirectly interlinked *Rhytidotheca*, *Penteune*, *Phymatocaryon* and *Pleioclinis* all of which are here associated with *Elaeocarpus* (Table 1).

Because Mueller possessed so wide a knowledge of the Australian Flora it is of interest to speculate as to why he created these 4 fossil genera. In discussions accompanying the generic descriptions, Mueller made it clear he was of the opinion that it was improper to assign fragmentary fossil material to extant genera. However, for *Penteune*, *Phymatocaryon* and *Rhytidotheca* he suggested affinities with Sapindaceae amongst living taxa thereby strengthening the view the fossil genera were related. His reasons for selecting the Sapindaceae are spelled out in the discussion accompanying the description of *Phymatocaryon* (Mueller, 1871a: 47). There he noted that the pendent seeds, locular dehiscence, drupaceous fruits ('with a distinct sarcocarp and putamen') are all family characters of the Sapindaceae. Furthermore, he observed that the fruits of some members of the family also have surfaces that exhibit 'tubercular roughness'. He may have been particularly swayed by this character since 5 years earlier he had described *Cupaniopsis tomentella* (F. Muell. ex Benth.) S. Reyn., fruits of which are described by Reynolds (1985) as 'valves, thick rugose, deeply wrinkled outside'.

Nonetheless Mueller was not entirely satisfied his fossil fruit genera all belonged in the Sapindaceae for a few months later he noted the similarity of *Rhytidotheca* to the fruits of *Flindersia* and *Chloroxylon* (Mueller, 1871b: 39) then placed in the Meliaceae. He discounted an

TABLE 1. The three principal characters stressed by Mueller in his original diagnoses of fossil fruit genera now associated with *Elaeocarpus*. Bracketed valve numbers designate the less common state(s); bracketed shape and sculptural designations comply with terminology used herein.

Genus	Valve number	Shape	Surface
<i>Penteune</i>	(4) 5 (6)	Ovate-globose to broadly ovate (spherical-prolate ellipsoidal)	Slightly rough-deeply wrinkled (pitted-verrucate/rugulate)
<i>Rhytidotheca</i>	5	Ovate (perprolate ellipsoidal)	Wrinkled (rugulate)
<i>Phymatocaryon</i>	2-3 (4)	Spherical to ovate (spherical-prolate)	Rough-deeply wrinkled (baculate/verrucate-rugulate)
<i>Pleioclinis</i>	(5-6) 7-9	Ovate globular-ovate (spherical-prolate)	Tubercular-rough (verrucate-rugulate)

affinity with the Sapindaceae because 'the number of fruit-valves, increased to five, remains exceptional'. Though most Sapindaceae have 3-loculate fruits there are many with fewer or more carpels and so it is surprising Mueller was so concerned on that account. Likewise, in his discussion of the affinities of *Penteune* he wrote, 'It belonged, however, most probably to Sapindaceae, although the possibility of it having formed a genus of the meliaceous order is not excluded' (Mueller, 1874a: 41).

Why Mueller failed to recognise the similarity of at least *Penteune* with fruits of *Elaeocarpus* is difficult to understand unless it stemmed from him being familiar, as is likely, only with fresh material that had been pressed or stored in preservative. In these circumstances the fruit stones do not disintegrate. They do so after prolonged exposure to wet/dry weathering cycles and/or degradation by fungi and/or insect attack. Under these circumstances disintegration of the stony mesocarp into segments may occur after loss of vascular tissue from the central cylinder and the radial strands that connect the central cylinder to the segment sutures. It is likely that fossil fruits were subjected to similar degradation processes during incorporation into sediments. Moreover, many of those from deep lead sediments have been pyritised, and oxidation after recovery and storage may cause the mesocarp segments to separate. Thus, Mueller was very likely distracted from the real identity of the fossil fruits because many dehiscence into segments as a result of burial, fossilisation, and subsequent retrieval and storage.

By 1884 Mueller was aware that *Rhytidotheca* fruits were considered consistent with those of *Elaeocarpus* because *R. johnstonii* F.Muell. (in Johnston, 1882) was based on material assigned by Ettingshausen (1883) to *E. bassii* Ettingsh. Nonetheless, he did not comment on or challenge Ettingshausen's assignment. Likewise it is surprising that Ettingshausen (1883: 63), having recognised that *E. bassii* and *R. johnstonii* were conspecific, relegated other species of *Rhytidotheca* (*R. lynchii*, *R. pleioclinis*) to *Incertae sedis* without comment. Furthermore, he did not suggest that *Penteune* and *Elaeocarpus* might be congeneric and followed Mueller in assigning the former to Sapindaceae (Ettingshausen, 1883: 16) rather than Tiliaceae in which at that time *Elaeocarpus* was included. In a lecture to the Royal Society of Tasmania, Mueller (1884) restated his argument (Mueller, 1871a) for not

including fossil leaves and other plant organs in extant genera.

The likely affinity of *Phymatocaryon mackayii* F.Muell., 1871 with *Elaeocarpus* was noted by Deane (1925) and confirmed by Kirchheimer (1935) after detailed comparison of fossils and mesocarps of extant *E. angustifolius*. Selling (1950) formally transferred several of Mueller's species to *Elaeocarpus* without comment. As noted by Selling (1950) transfer of *Rhytidotheca lynchii*, *Penteune clarkei*, *P. allportii*, *P. brachyclinis*, and *P. trachyclinis* to *Elaeocarpus* rendered *Penteune* and *Rhytidotheca* superfluous. Rozefelds (1990) and Rozefelds & Christophel (1996a, b; in press) provided evidence for reference of several fossil fruit taxa to *Elaeocarpus*. These include *E. clarkei*, *E. spackmaniorum*, *E. cunningii*, and *E. mackayii*. However, they expressed doubts about a relationship, as suggested by Selling (1950), of *Rhytidotheca lynchii*, *Penteune trachyclinis*, and *Phymatocaryon angulare* with *Elaeocarpus*.

MATERIAL

Fruits reported upon here include charcoallified material from subsurface sediments near Moranbah and Blackwater in central Queensland and permineralised material from Glencoe (Rozefelds, 1990; Rozefelds & Christophel, 1996b, in press) that are held in the Queensland Museum (QMF); charcoallified and lignified fruits in the Australian Museum (AMF), the Department of Mines, Geological Survey of New South Wales (MMF), and the Museum of Victoria (NMVP). The last mentioned collection includes most of Mueller's Victorian material originally housed in the Geological Survey of Victoria. Mueller's material came from deep lead sediments in Victoria and New South Wales and specimens illustrated by Mueller have been identified for most of his Victorian species. Mueller's New South Wales material may have been destroyed in the Garden Palace fire in 1882 which included 'the palaeontological specimens of the recently deceased Reverend W.B. Clarke' (Gilbert, 1986: 107). Clarke collected several of the fruits described by Mueller from New South Wales. The repository of type material of *E. muelleri* Ettingshausen, 1886 is also unknown. Tasmanian material attributed to *E. bassii* by Ettingshausen (1883) and to *Penteune allportii* and *Rhytidotheca johnstonii* by Mueller (in Johnston, 1882) has not been located. Other material not examined includes *Rhytidotheca major* Deane, 1925 and *E. cerebriformis* Rozefelds & Christophel, 1996b.

LOCALITIES. (Fig. 1).

Queensland. a) Picardy Station, near Moranbah $21^{\circ}5'17.6''\text{S}$ $147^{\circ}50'34.3''\text{E}$. Holes RDPD98MA 17, 111-133m and RDPD98MA21, 123-133m. Fruits were recovered from both boreholes from near the base of a thin sequence of sands and silts with interbeds of lignites that occur beneath basalts and overlie Permian Coal Measures (Fig. 2A). The basalts are probably related to those of the Nebo Province dated as 30-34 Ma. (Wellman & McDougal, 1974, Sutherland pers. comm.), but stratigraphic relationships between these and those intersected in the boreholes have not been established. Host sediment was not retained for palynological assessment. Thus, the minimum age is tentatively suggested as Early Oligocene.

b) Near Blackwater $24^{\circ}1'1.3''\text{S}$ $148^{\circ}48'50''\text{E}$. South Blackwater Coal Pty Ltd Hole R8736, 82m. Fruits are from ligneous bands within sands that underlie basalts and overlie Permian sediments (Fig. 2B). Basalts to the SW in the Springsure area are dated at 27-33Ma. (Sutherland et al., 1977), but stratigraphic relationships between dated basalts and those in borehole R8736 are uncertain. Moreover, no sediment was available for palynological analysis and a minimum age of Early-Late Oligocene is tentatively indicated.

c) Glencoe Station ($23^{\circ}36'\text{S}$ $148^{\circ}06'\text{E}$), near Capella (Rozefelds, 1990; Rozefelds & Christophel, 1996a, in press). These occur in silcretes that overlie undated basalts. However, volcanics near Emerald are dated as 30-32Ma. and those southwest of Capella at 26Ma. imply a maximum Oligocene age, possibly Late Oligocene-Early Miocene according to Rozefelds (1990).

New South Wales. *Elaeocarpus*-type fruits are known from a scatter of localities on the western flanks of the eastern highlands of northern and central New South Wales (Fig. 1).

a) Newstead near Elsmore ($29^{\circ}47'\text{S}$, $151^{\circ}17'\text{E}$), Ettingshausen (1886) described *E. muelleri* fruits from ironstones overlain by basalts. Pickett et al. (1990) concluded an Early Miocene or younger age based on K-Ar dates of $20.5 \pm 0.2\text{Ma.}$ for a nearby basalt flow.

b) At Witherden's Tunnel, near Emmaville leaf fossils attributed to *E. muelleri* were recorded from carbonaceous clays and silts beneath basalts ($30.4 \pm 0.3\text{Ma.}$); palynological dates confirm a Late Eocene age (Pickett et al., 1990). However, there is no evidence to suggest that the leaf and

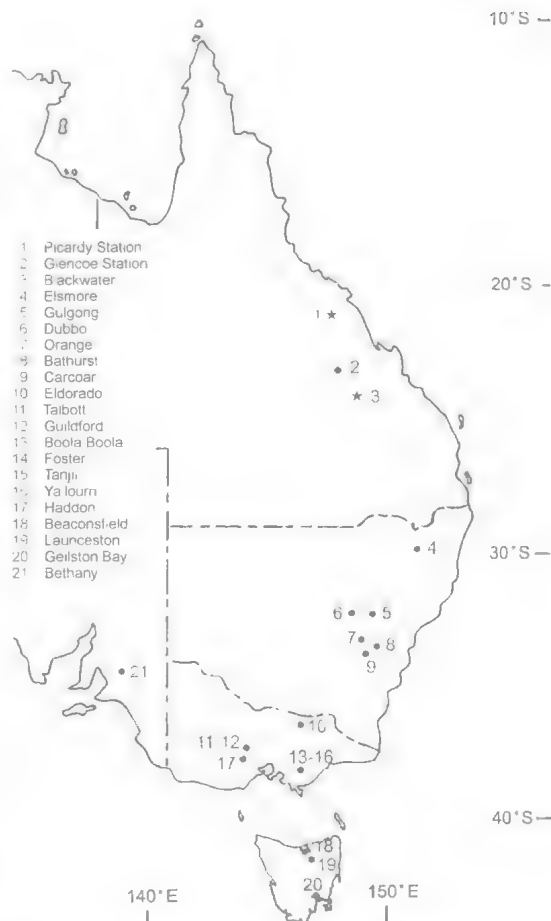


FIG. 1. Map of Australia showing localities from which fossil fruits of *Elaeocarpus* have been reported.

mesocarp fossils from the separate localities derived from the same plant taxon.

c) Gulgong district ($32^{\circ}12'\text{S}$, $149^{\circ}32'\text{E}$) sites include Home Rule Lead and Black Lead (Mueller, 1876, 1877, 1879). The leads are sediment fills of palaeodrainage channels on Palaeozoic basement and are overlain by basalt flows. Isotope ages (K-Ar) of the basalts range from $13.8 \pm 1.2\text{Ma}$ to $14.8 \pm 1.2\text{Ma}$. (Dulhunty, 1971; Meakin & Morgan, 1999). The Home Rule Lead is assigned to the Middle Miocene *Triporopollenites bellus* Zone (McMinn, 1981) in agreement with isotope dates.

d) At Orange ($33^{\circ}17'\text{S}$, $149^{\circ}06'\text{E}$), Carcoar ($33^{\circ}37'\text{S}$, $149^{\circ}08'\text{E}$), and Bathurst ($33^{\circ}25'\text{S}$, $149^{\circ}35'\text{E}$) charcoallified fruits are known from beneath basalts in numerous deep leads and reef mines. As at Gulgong the sediments are overlain

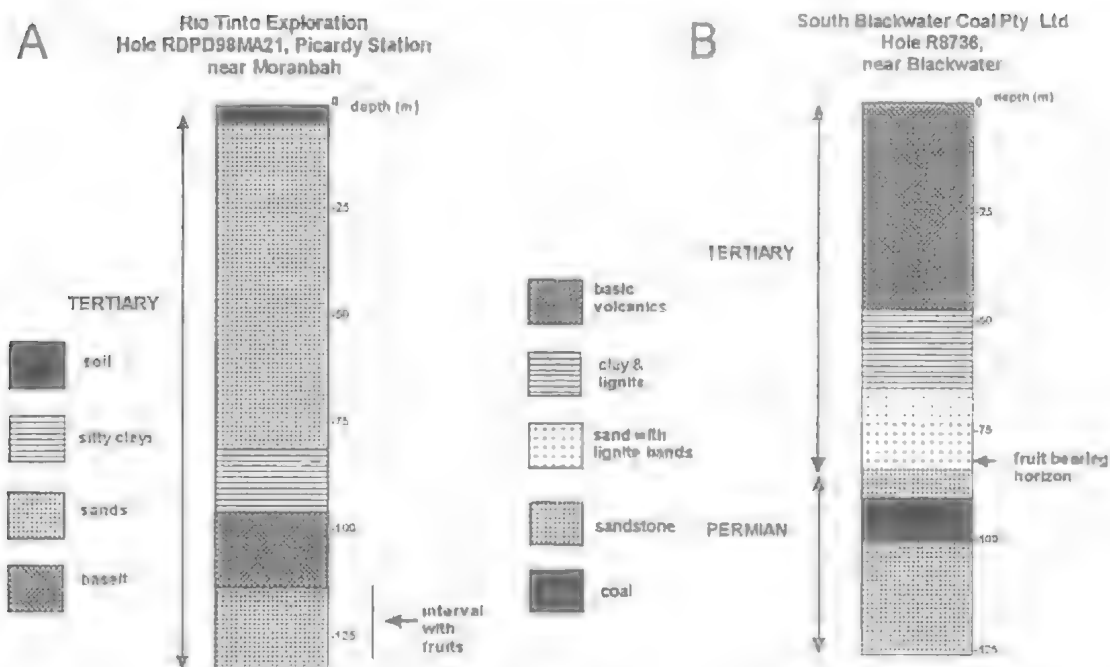


FIG. 2. Stratigraphic sequences and sampling horizons in: A, Hole RDPD98MA21, Picardy Station near Moranbah, Queensland; and B, South Blackwater Coal Pty Ltd Hole R8736 near Blackwater, Queensland.

by basalts that were extruded from Mt. Canabolas SW of Orange. Basalts that overlie the sediments at Forest Reefs and in the Lucknow Mine have provided dates of 11.2–13 Ma., late Middle-early Late Miocene (Johnson, 1989).

Victoria. Fossil fruits have been collected from buried placer deposits in the Murray, Gippsland and Otway Basins, and on the northern flanks of the Great Divide. There are few data on precise ages of the deep lead sediments.

a) The Eldorado deep lead (Ted Ovens G & TM Co. Shaft), Beechworth (37°18'S 146°32'E), in the Murray Basin, (Mueller, 1874c: fig. 2) is of unknown age. Palynological dates on other Murray Basin deep leads near Stawell, W Victoria and in the Woodstock 10008 bore near Bendigo, Victoria, indicate Oligocene and late Early Miocene ages based on reference of the former to the lower *Proteacidites tuberculatus* spore-pollen Zone and of the latter to the upper part of that zone (Partridge & Wilkinson, 1982; Partridge, 1993).

b) The bulk of fruits described by Mueller were obtained from deep lead sediments at Smythe's Creek (Reform Co. Shaft) and Nintingbool (Crucible Co. Shaft), near Haddon (37°18'S 146°32'E), SW of Ballarat. Silty sands of the 'wash dirt' overlying basement near the bottom of the shafts (Reform Co. Shaft, ~47.5m (156ft);

Crucible Co. Shaft, ~23.2m (76ft)) are designated as the source of the fruits (Mueller, 1874c: 29, Map 1), and in the Reform Shaft the sediments are beneath basalts. Dates of 2–5 Ma. have been obtained from basalts that overlie alluvial sediments in the Ballarat district (Sutherland, 1995) and palynofloras recovered from sediments intercalated between two of the flows indicate the *Tubulifloridites pleistocenicus* spore-pollen Zone of late Pliocene to Pleistocene age (Partridge, 1995). The minimum age of the subbasaltic sediments is thus Late Miocene age, but Rozefelds & Christophel (1996b) argue for an Early-Middle Miocene age based on association of the fruit *E. mackayii* (F. Muell.) Kirchheimer, *E. clarkei* (F. Muell.) Selling, and *Spondylostrobus symthii* F. Muell. (see also Greenwood et al., 2000). Unfortunately, Mueller did not always specify precise depth or mine shaft for localities at Haddon.

c) Gippsland Basin deep lead sediments at Talbot (37°10'S 146°14'E), Foster (37°10'S 146°14'E) and Tanjil (38°01'S 146°14'E). Thus far, the ages of these have not been resolved, but as for the Haddon sediments Rozefelds & Christophel (1996b) suggest an Early-Middle Miocene age.

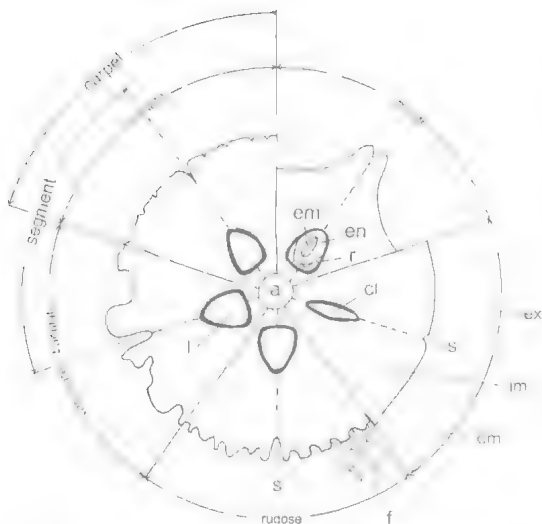


FIG. 3. Stylised transverse section of *Elaeocarpus* fruit in which each of the 5 carpels has different surfical sculpture of the inner mesocarp. a, axis; cl, compressed locule; e, endocarp; en, endosperm; em, embryo; ex, exocarp; f, fibres; im, inner mesocarp; om, outer mesocarp; l, locule; r, raphe; s, suture.

d) Yallourn Coal Measures, Yallourn (38°10'S 146°21'E) in the Yallourn Formation within the *Triporopollenites bellus* spore-pollen Zone of late Early-Late Miocene age (Rozefelds & Christophel, 1996b).

South Australia. Fruits from subsurface sediments near Bethany (34°32'S 139°00'E) in the Barossa Basin (Paterson in Hossfeld, 1949) occur in the Rowland Flat Sand, a lignitic facies overlain by coarse-grained fluviolacustrine sand and gravel fining upwards to bedded silt and clay. Palynological dates are Early Oligocene-Early Miocene for the basal sediments and Early-Late Miocene for coarser upper facies (Alley, 1995).

Tasmania. Deep lead sediments at Brandy Creek, Beaconsfield (41°12'S 148°49'E) and outcrops at Launceston (41°27'S 147°10'E). A mid-Tertiary (Oligocene) age is indicated for these localities based on palynofloras of sub-basaltic sediments in the Tamar Graben (Forsyth, 1989).

b) Calcareous fruits from Geilston Bay, Hobart (41°12'S 148°49'E) occur in travertine which is equivalent in age to nearby basalts dated as 22.4 Ma, Early Miocene (Tedford et al., 1975).

New Zealand. a) At Mangonui (35°00'S 173°20'24"E), north of Auckland, charcoalfied fruits occur Mangonui Formation lignites (Late Miocene) associated with *Cocos zeylandica* Berry (Berry, 1926; Thompson, 1978; Isaac et al. 1994).

b) At Schultz Creek (42°16'48"S 171°07'12"E), north of Greymouth, South Island lake sediments deposited during the last interglacial (100Ka.) have yielded fruits comparable to those of extant *E. dentatus* (Burrows, 1997). The material illustrated has been deposited at the Queensland Herbarium.

METHODS

Charcoalified specimens were photographed after whitening with ammonium chloride; internal characters including those of the locules were photographed without whitening. Mueller's type specimens are figured together with reproduction of the original lithographic illustrations, the latter of which represent mirror images. Available seed coats were examined in transmitted light after clearing in chromium trioxide for several hours, followed by thorough washing in distilled water after which they were mounted on glass microscope slides in glycerine jelly.

Fruit stones of extant *E. angustifolius* Blume and *E. reticulatus* Smith were collected from trees growing at the Brisbane Botanic Gardens, Mt Coot-tha and the University of Queensland.

SYSTEMATIC PALAEOBOTANY

Elaeocarpus L.1753

Rhytidotecha F.Muell., 1871:39.
Phymatocaryon F.Muell., 1871:41.
Penteune F.Muell., 1874a:3941.
Pleioclinis F.Muell., 1882:43

TYPE SPECIES. *Elaeocarpus serratus* L.

FRUITS OF EXTANT ELAEOCARPUS. In extant *Elaeocarpus* fruits develop from flowers with a superior 2-8 (usually 3-5) loculate ovary that terminates in a single style surmounted by a lobed stigma. There are 2-12 anatropous ovules per locule and these are attached to an axile placenta. When there are few ovules per locule they are attached high up on the axis and so appear to be subapical (Figs 4, 6B,C). Only one ovule per locule develops into a seed and in some species there is only 1 seed per fruit. Expansion of this 1 seed usually results in compression of the adjoining seedless locules (Figs 4, 5D,G).

The fruit is a drupe, a useful term, ill-defined but widely used in the literature (Clifford & Dettmann, in press). In most species the fruit surface is iridescent blue, the colour due 'not to a blue pigment, but by the structure of the cuticle which reflects blue light' (Lee, 1991). The outer fleshy mesocarp is usually thin and densely

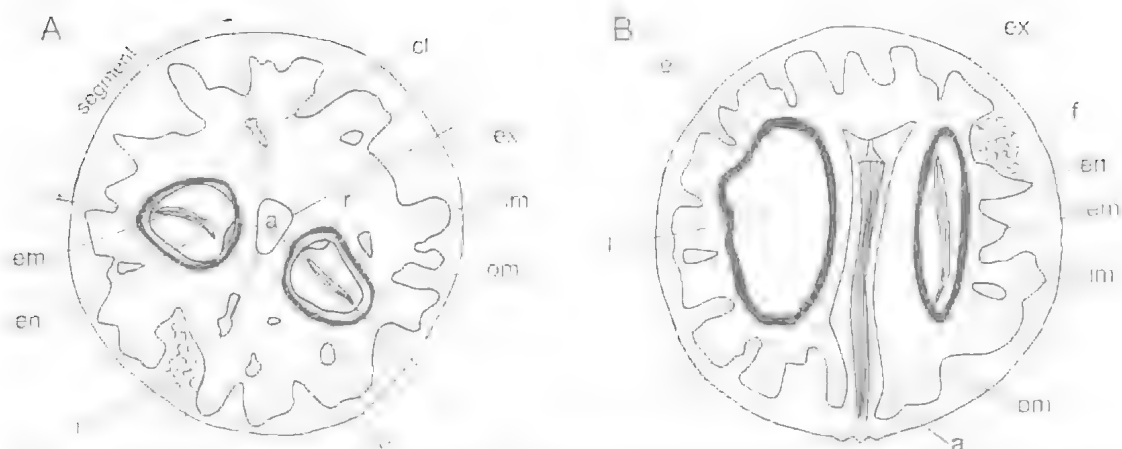


FIG. 4. Sections through *Elaeocarpus angustifolius* Blume fruits: A, transverse; B, vertical. Labels as for fig. 3.

fibrous, fibres intertwined with the sculptured surface of, or extending into, the woody inner mesocarp (Fig. 5A). The latter encloses the locules and their surrounding endocarps to form a stone whose outer surface may be smooth, pitted, fossulate, rugulate, baculate, verrucate, or echinate. At maturity the vascular strands of the axis decay, resulting in a hollow cylinder which extends for ~ two-thirds the length of the mesocarp from its proximal end (Figs 3, 4, 5F). Further decay of radially disposed strands beneath the segment sutures results in the mesocarp and enclosed endocarps splitting vertically between the septa to produce segments that expose seeds or aborted ovules on their radial walls (Fig. 5G-I). As was recognised by Mueller, such dehiscence is loculicidal. The lines along which the mesocarp split are usually clearly marked by vertical sutures on the surface of the mesocarp (Fig. 5A-C) and each segment consists of a woody, inner mesocarp, half of 2 adjacent endocarps and associated locules (Fig. 5H,I). The inner surface of the endocarp may bear multicellular scales and hairs (Corner, 1976).

Seeds are fusiform, bitegmic with glabrous or hairy surfaces. The testa is several cells thick with an outer epidermis of elongate to isodiametric cells (Figs 6I, 7F) that in some species are lignified. The tegmen is multiplicative, the outer epidermis of which has fibriform, bulbous or dumb-bell shaped, lignified sclereids that are arranged longitudinally (Fig. 5G,I). Both the testa and tegmen are vascularised in the chalaza which forms the woody basal and acute prominence of the seed (Corner, 1976).

Shape, structure and surface sculpture of the fruit stones are useful species discriminators

(Rozefelds & Christophel, 1996a). However, such features have been little utilised and remain largely undocumented in current infrageneric classifications. Moreover, little attention has been accorded anatomical features of the inner mesocarp wall and the enclosed endocarps.

The only record of fossil mesocarps attributable to an extant species is that of *E. dentatus* stones in interglacial (100Ka) sediments from New Zealand (Burrows, 1997).

FOSSIL FRUITS. The following fossil taxa are considered congeneric with *Elaeocarpus*.

PENTEUNE F. Muell., 1874; type species (designated here) *Penteune clarkii* F. Muell., 1874a: 41 from Elsmore, NSW; Early Miocene: Neotype (designated Rozefelds & Christophel, 1996a: 43), NMVP53913, Fig. 11A, B; Mueller's figured specimens from Haddon (Smythe's Creek, ?Reform Co. Shalt, ~47.5m) are believed lost (Rozefelds & Christophel, 1996a: 43). Species included: *P. allportii* F. Muell., in Johnston 1882: figs 40, 41, 44-47. *P. brachyclinis* F. Muell., 1874a: 41, pl. 8, figs 1-9. *P. trachyclinis* F. Muell., 1874a: 41, pl. 8, figs 10-17.

PHYMATOCARYON F. Muell., 1871; type species *Phymatocaryon mackayi* F. Muell., 1871a: 41 (by monotypy) from Haddon (Smythe's Creek, Reform Co. Shalt, ~47.5m), sediments beneath basalts; ?Early-Middle Miocene: Lectotype (designated Rozefelds & Christophel (in press)) NMV53562, Mueller 1871a: 41, pl. 2, fig. 4;

Species included: *P. angulare* F. Muell., 1874b: 41, pl. 10, figs 1-4. *P. bivalve* F. Muell., 1877: 180, 1878: 39, pl. 15, figs 6-9.

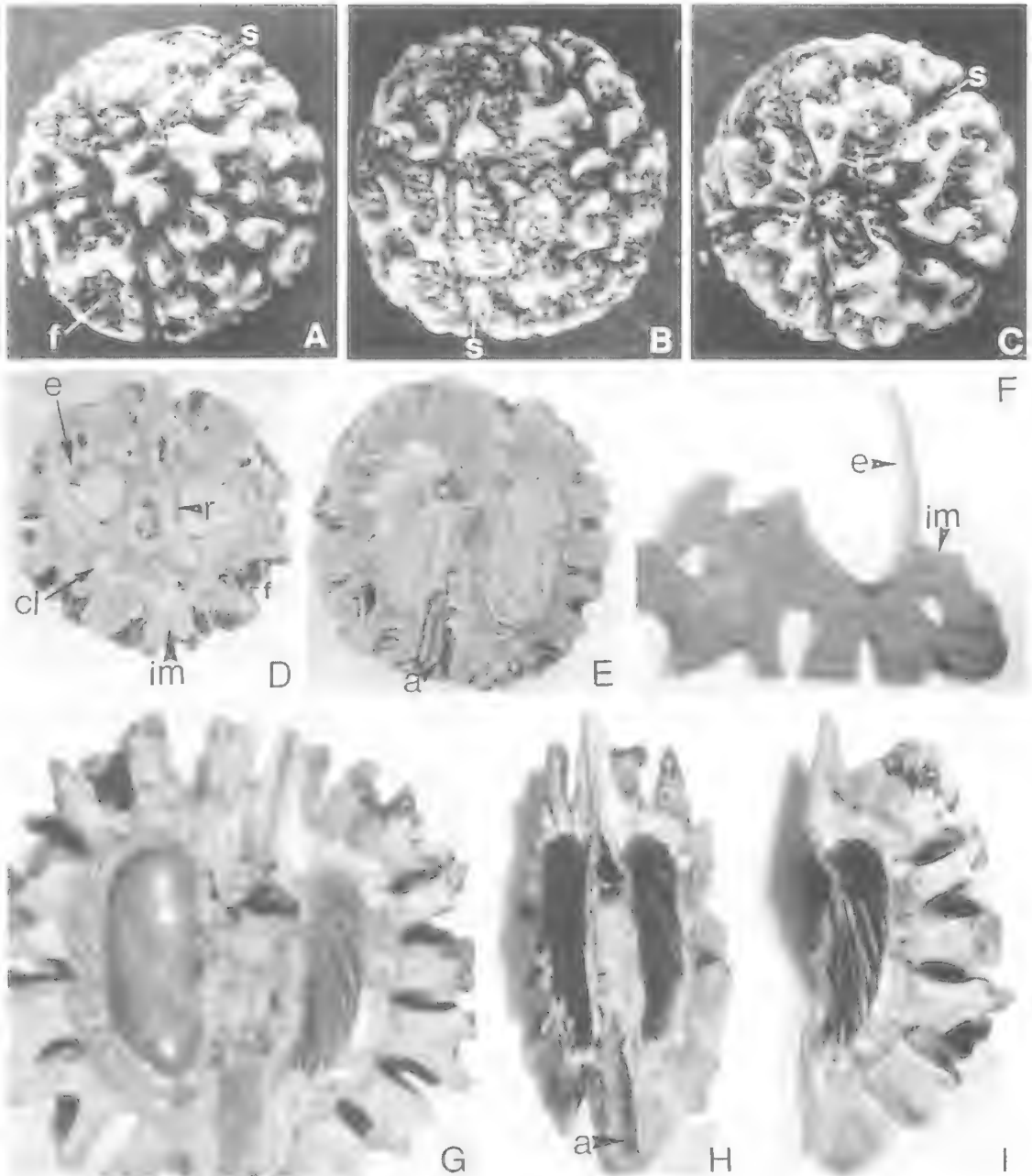


FIG. 5. Fruit stones of *Elaeocarpus angustifolius* Blume. A-C, apical, lateral, and basal views showing sculpture of woody inner mesocarp with attached fibre (f) bundles and sutures, $\times 2$. D, photograph of transverse section in Fig. 4A of fresh, mature fruit stone showing sculptured woody inner mesocarp with fibre (f) bundles on the surface, enclosed endocarps, two with fertile locules containing seeds, each showing the raphe, the other three locules compressed, $\times 2$. E, photograph of vertical section in Fig. 4B showing vascular strands in the axis, $\times 2$. F, vertical section portion of inner mesocarp removed to reveal closely adpressed endocarp, $\times 4$. G, internal view of two segments of partially rotted mature fruit stone showing seed in fertile locule (left), compressed sterile locule (right), and hollow axis, $\times 4$. H, I, internal views of dehiscent segment comprising inner mesocarp with halves of two adjacent locules and endocarps showing ridges and grooves on their inner surface, $\times 4$. Labels as for Fig. 3.

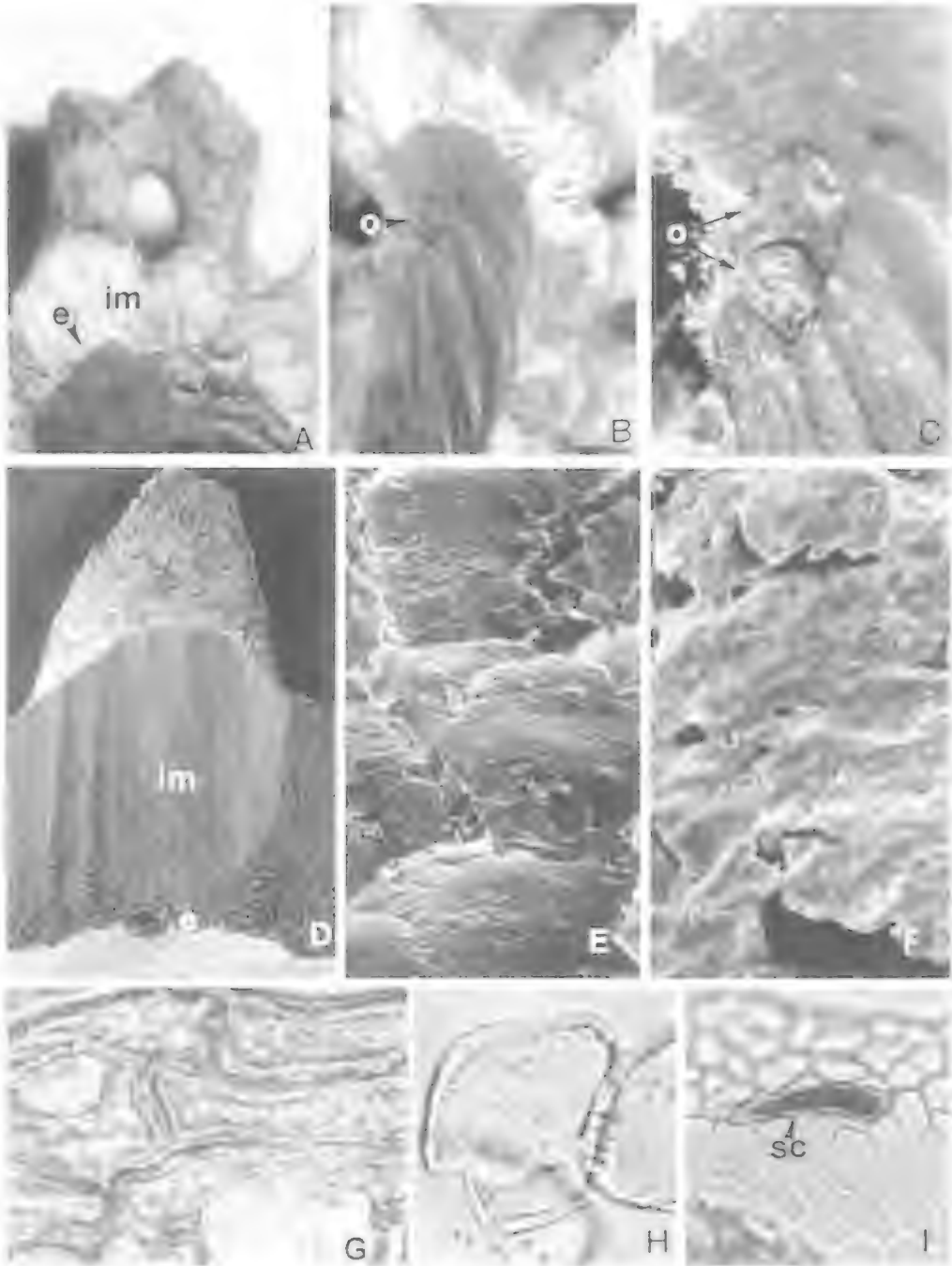


FIG. 6. Micrographs of fruit stones of *Elaeocarpus angustifolius* Blume. A, transverse section of inner mesocarp and endocarp walls, and profile of a concave-crested, arched sculptural element at outer surface of inner mesocarp, $\times 10$. B, C, detail of compressed locule with 2 near-apical, axially attached, aborted ovules (o), and showing coalescence in the apical region of locule of ridges and grooves on inner surface of endocarp, $\times 10$, and $\times 25$ respectively. D, scanning electron micrograph of section of inner mesocarp and endocarp, $\times 30$. E, F, scanning electron micrographs of outer surface and transverse section of inner mesocarp, $\times 2000$ and $\times 4000$ respectively. G, outer epidermis of tegmen showing elongated sclereids with thick, pitted walls, $\times 750$. H, subspherical sclereid from tegmen, $\times 500$. I, outer cuticle of testa, with a sclereid (sc) arrowed derived from outer epidermis of tegmen, $\times 250$. Labels as for Fig. 3.

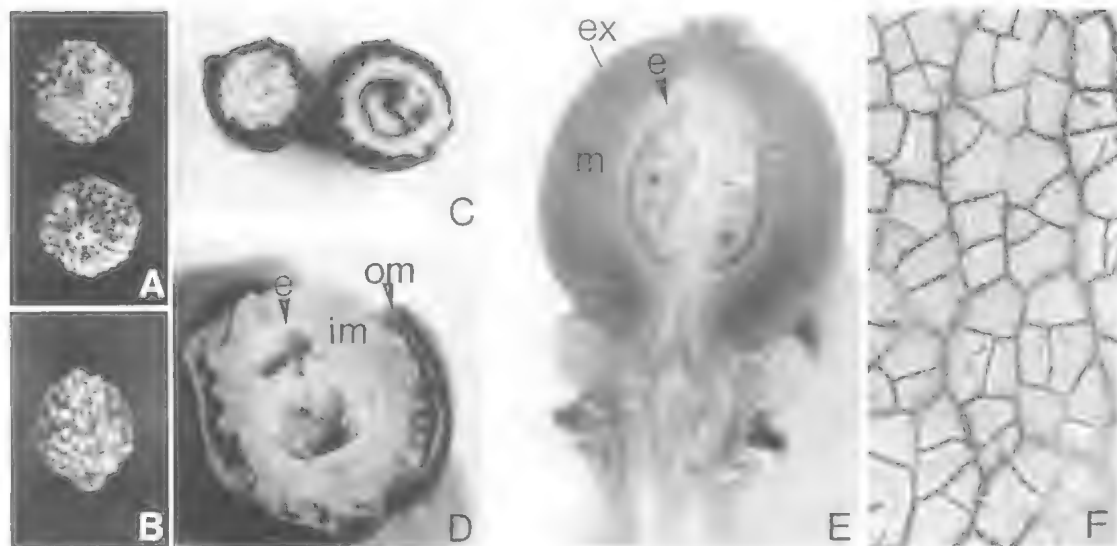


FIG. 7. Fruits, fruit stones and seeds of *Elaeocarpus reticulatus* Smith. A, apical (upper) and basal (lower) views of fruit stone, $\times 2$. B, lateral view of fruit stone, $\times 2$. C, vertical (left) and transverse (right) sections of immature fruits, $\times 2$. D, transverse section of fruit with outer mesocarp partially detached (left) revealing surface sculpture of inner mesocarp, $\times 6$. E, vertical section of immature fruit showing axile placentation and axial tissue, $\times 16$. F, outer cuticle of testa, $\times 250$. Labels as for Fig. 3.

PLEIOCLINIS F.Muell., 1882; type species *Pleioclinis couchmanii* F.Muell., 1882: 43 (by original designation) from Haddon (Smythe's Creek or Nintingbool), sediments beneath basalts; ?Early-Middle Miocene; Lectotype (here designated). NMVP53920, Mueller 1882: 41; pl. 19, figs 9, 10; Species included: *Rhytidotheca pleioclinis* F.Muell., 1873), (= *P. shepherdi* F.Muell., 1882; junior objective synonym)

RHYTIDOTHECA F.Muell., 1871; type species *Rhytidotheca lynchii* F.Muell., 1871b: 39 (by monotypy) from Haddon (Nintingbool, Crucible Co. Shaft, ~23.2m), deep lead sediments; ?Early-Middle Miocene.

Lectotype (here designated). NMVP6034, Mueller, 1871b: 39, pl. 4, fig. 4 (right hand segment) and NMVP6033, Mueller, 1871b: 39, pl. 4, fig. 1, centre segment broken at apex.

Species included: *R. johnstonii* F.Muell. in Johnston, 1882: 50, fig. 6. *R. major* Deane, 1925: 491, pl. 60, fig. 12 (nomen nudum). *R. pleioclinis* F.Muell., 1873: 42, pl. 6, figs 1-4.

REMARKS. Recognition of fossilised *Elaeocarpus* stones has been based on sculpture, shape, locule number, and position of seed attachment (Deane, 1925; Kirchheimer, 1935; Selling, 1950; Rozefelds, 1990; Rozefelds & Christophel, 1996a, b, in press). Woody mesocarps of *Elaeo-*

carpus are distinguished from other *Elaeocarpaceae* by: a pitted, smooth, fossulate, verrucate, baculate, echinate or rugose surface with longitudinal sutures that delimit segments; 2-9 carpels; passive loculicidal dehiscence into segments; 1-seeded locules; fertile and sterile locules, the latter often compressed; ovules anatropous, pendulous with a ventral raphe; seeds fusiform with a multiplicative tegmen, the outer epidermis with pitted and lignified longitudinal cells. Further characters with apparent interspecific significance include the internal organisation and structure of the woody inner mesocarp and subjacent locules as revealed by extant *E. angustifolius* and *E. reticulatus* (Figs 5-7). In *E. reticulatus* young fruits have an axial column of elongated vascular strands (Fig. 7E). The inner mesocarp consists of isodiametric stony cells, and the enclosed endocarps comprise lignified cells, elongated and arranged tangentially. Fruits of *E. angustifolius* are similar in their organisation (Figs 5, 6). Fruit stones allowed to rot on the ground decompose slowly, but after time they may split into segments. Those of *E. angustifolius* were little affected after subjecting them to conditions that may be expected in a medium-high energy depositional situation. Stones agitated with sand, gravel and water in a closed container on a rotary shaker for 1 week showed no signs of breakage or abrasion of the

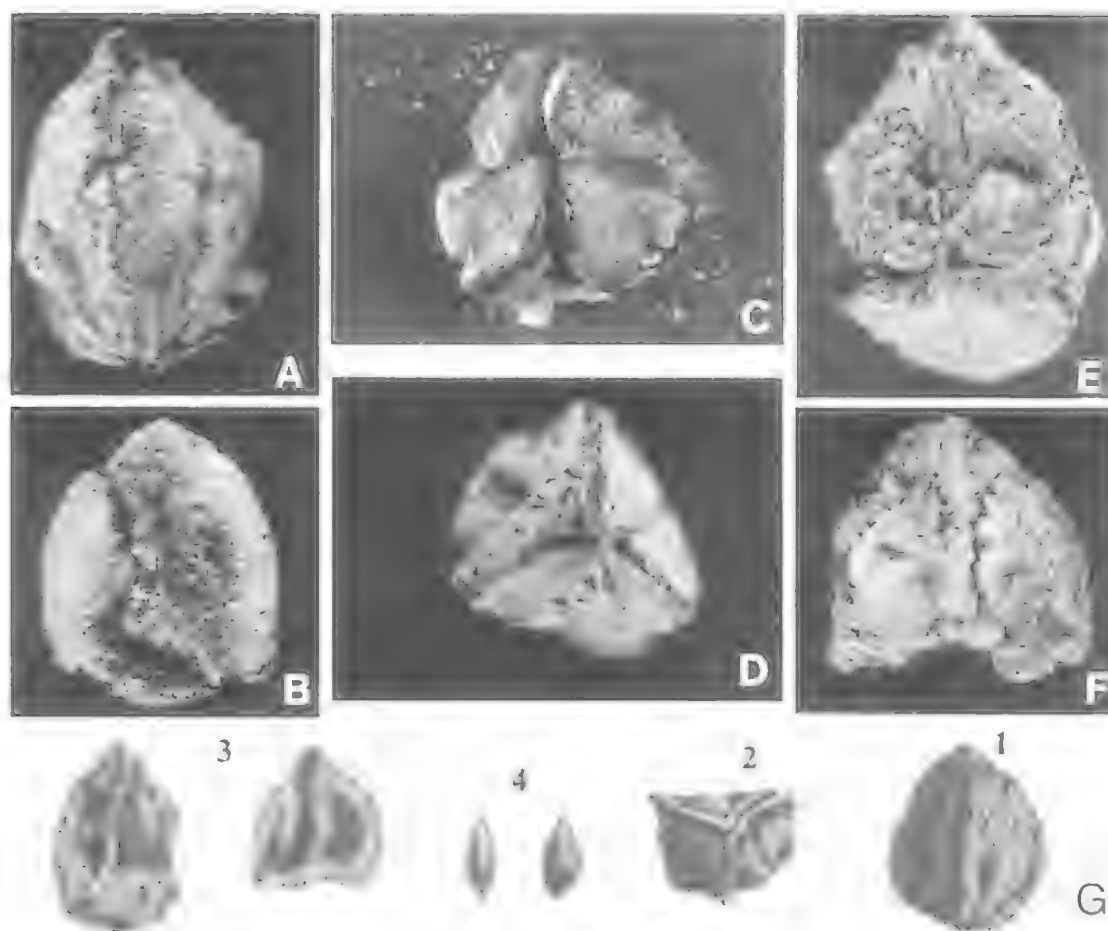


FIG. 8. *Elaeocarpus angularis* (F. Muell.) Selling, fruit stone. A-G, holotype. A, E, lateral views of external and internal surfaces of 2 segments and basal part of third segment (NMVP53565), $\times 2$. B, F, lateral views of external and internal surfaces of upper part of third segment (NMVP6017), $\times 2$. C, D, apical and basal views of whole fruit stone, $\times 2$. G, holotype as illustrated by Mueller (1874b, pl. X, figs. 1-4), but note his images are reversed and seeds represented in his fig. 4 have not been located.

external sculptural elements. However, after drying some dehisced into segments.

***Elaeocarpus allportii* (F. Muell.) comb. nov.**

Penteune allporti F. Muell. in Johnston, 1880a: 27 (nom. nud.).

Penteune allporti F. Muell. in Johnston, 1880b: 85 (nom. nud.).

Penteune allporti F. Muell. in Johnston, 1882: figs 40, 41, 44-47.

MATERIAL. LECTOTYPE (here designated): Whole specimen (Johnston, 1882, figs 40-41) and 4 of its segments (Johnston, 1882, figs 44-47) from Early Miocene Geilston Travertine at Geilston Bay, Tasmania. Stony mesocarp prolate (20mm long, 16mm wide), broadly elliptical in longitudinal section and circular in transverse section; 5-loculate (illustrated as 6-loculate but in

Johnson's Explanation of Figure corrected to 5-loculate). External surface punctate and with 5 longitudinal sutures; preserved mesocarp wall 2-3mm thick. Seed cavity fusoid, apically acute, 14mm long, 5mm wide.

DESCRIPTION. As for lectotype.

REMARKS. No description of calcereous specimens included in the species was provided, but Johnston (1882, Explanation of Figures) illustrated what he believed to be 'probably *P. allporti* F. Muell, F.v.M., m.s.' Mueller (1874a: 41) noted, under *Penteune clarkei* F. Muell., that 'an extremely similar fossil has been discovered in Tasmania by Morton Alport (sic), Esq., at Gerlston-Bay (sic) in tertiary travertine'. Selling (1950) suggested inclusion of *P. allportii* in

Elaeocarpus, but did not formally make the transfer.

COMPARISON. May be synonymous with, *E. clarkei* (Johnston, 1880b; Mueller, 1874a: 41).

DISTRIBUTION. Geilston Bay, Beaconsfield (Brandy Creek), Tasmania (Johnston 1880a,b, 1882).

AGE RANGE. Oligocene-Early Miocene.

AFFINITY. Possibly with *E. bancroftii* F.Muell. & Bailey.

***Elaeocarpus angularis* (F.Muell.) Selling, 1950**
(Fig. 8A-E)

Phymatocaryon angulare F.Muell. 1874b: 41, pl. 10, figs 1-4.
Elaeocarpus angularis (F.Muell.) Selling 1950: 558.

MATERIAL. HOLOTYPE (by monotypy): NMVP53565 (2 segments plus basal part of third) and NMVP6017 (upper part of third segment) (Fig. 8A-E) from ?Early-Middle Miocene at ~47.5m in Reform Co. Shaft at Smythe's Creek, Haddon, Victoria. Preserved mesocarp ovoid (22mm long, 19mm wide), oval acuminate in longitudinal section and convexly triangular in transverse section; 3-loculate and with 2 equally developed locules exposed, one of which contained a seed now lost. External surface with 3 longitudinal sutures embedded in protruding ridges that extend from base to apex; intervening surface with low relief striations and pits that may be artefacts of abrasion. Mesocarp wall 2-3mm thick with isodiametric cells; endocarp ~0.5mm thick, composed of tangentially aligned cells. Central axis of mesocarp composed of a hollow cylinder of elongated vascular strands that extend from stalk scar to near the apex. Seed cavity fusoid, the apex acute, 10-12mm long, 3-4mm wide. Seeds fragmented, anatomical detail not determined.

DESCRIPTION. As for holotype.

REMARKS. Additional material reported from NSW (Mueller, 1883) has not been located.

COMPARISON. *E. angularis* is similar in size and mesocarp sculpture to *E. (Penteune) brachyclinis*, but was distinguished on its 3 rather than 5 locules (Mueller, 1874b). With 3 locules and position of the seed the taxon was accommodated in *Phymatocaryon* (Mueller, 1874b: 42). *E. (Phymatocaryon) bivalve* was separated from *E. angulare* on its 2 segments (valves sensu Mueller), the edges of which are acute and wing-like and in which the sutures are embedded (Mueller, 1877, 1878). Moreover, in *E. bivalve* 1 of the 2 locules is compressed, unlike *E. angularis*.

DISTRIBUTION. Haddon (Smythe's Creek, ?Reform Co. Shaft, ~47.5 m), Victoria; Beneree, Dubbo, NSW (Mueller 1874b, 1883).

AGE RANGE. ?Early-Late Miocene.

AFFINITY. As suggested by Selling (1950) with *Elaeocarpus*. However, the lectotype has equally developed locules and the seed coat structure is unknown; an affinity with the Euphorbiaceae is possible (Rozefelds pers. comm.).

***Elaeocarpus bivalve* (F.Muell.) comb. nov.**
(Fig. 9A-L)

Phymatocaryon bivalve F.Muell. 1877: 180.
Phymatocaryon bivalve F.Muell. 1878: 39, pl. 15, figs 6-9.
Phymatocaryon bivalve F.Muell. 1879: 170, pl. 3, fig. 2.
Phymatocaryon bivalve F.Muell. 1883: 9, pl. 15, figs 6-9.

MATERIAL. NEOTYPE (here designated): MMF36220. (Fig. 9A-C) from the late Middle - early Late Miocene Black Lead at Gulgong, NSW. Mesocarp woody, ovoid, vertical axis 17mm, lateral axes 14 and 21mm; with 2 segments delimited by a longitudinal suture and reflexed at their margins; locules 2, one with a near apical seed, the other compressed; dehiscence loculicidal. Mesocarp wall 4mm thick, compact, with a near smooth undulating outer surface. Locules about the central axis of vascular strands arranged in a hollow cylinder that extends from the stalk scar to near the apex. Endocarp composed of tangentially oriented elements with shortly stalked bifid hairs on the inner surface. Seed cavity ovoid, 10mm long, 4-5mm wide.

DESCRIPTION. Fruit stones woody ovoid, vertical axis 17-20mm, lateral axes 13-16mm and 17-22mm; with 2 segments delimited by flanged and reflexed margins adjacent to the longitudinal sutures; locules 2, one of which is usually compressed, the other with a near apical seed. Mesocarp wall 3.5-6mm thick at segment margin, compact, and with a near smooth undulating outer surface. Locules about the central axis of vascular strands arranged in a hollow cylinder extending from the stalk scar to near the apex. Endocarp of tangentially oriented elements. Seed cavity ovoid, twice as long as wide; seed with near apical attachment. Seed coat near smooth, testa with outer cuticle of rectangular cells up to 30µm long, 20µm wide. Tegmen with outer epidermis of elongated, bulbous cells (up to 100µm long, 40µm wide) with pitted, lignified walls 2-4µm thick. Several layers of underlying layers composed of thin-walled (<1µm thick) cuboid cells.

REMARKS. Seed morphology and attachment and seed coat structure of the species is consistent with *Elaeocarpus*. A neotype is designated because the original type series (Mueller 1877, 1878) and those figured by Mueller (1879) have not been located, almost certainly destroyed a century ago. Mueller's specimens illustrated in 1878 have a less prominent flange than those depicted in 1879. New Zealand specimens attributed by Berry (1926) are too abraded for positive identification (Rozefelds, pers. comm.).

COMPARISON. *E. bivalve* is 2-loculate and with imperfect bilateral symmetry with respect to the

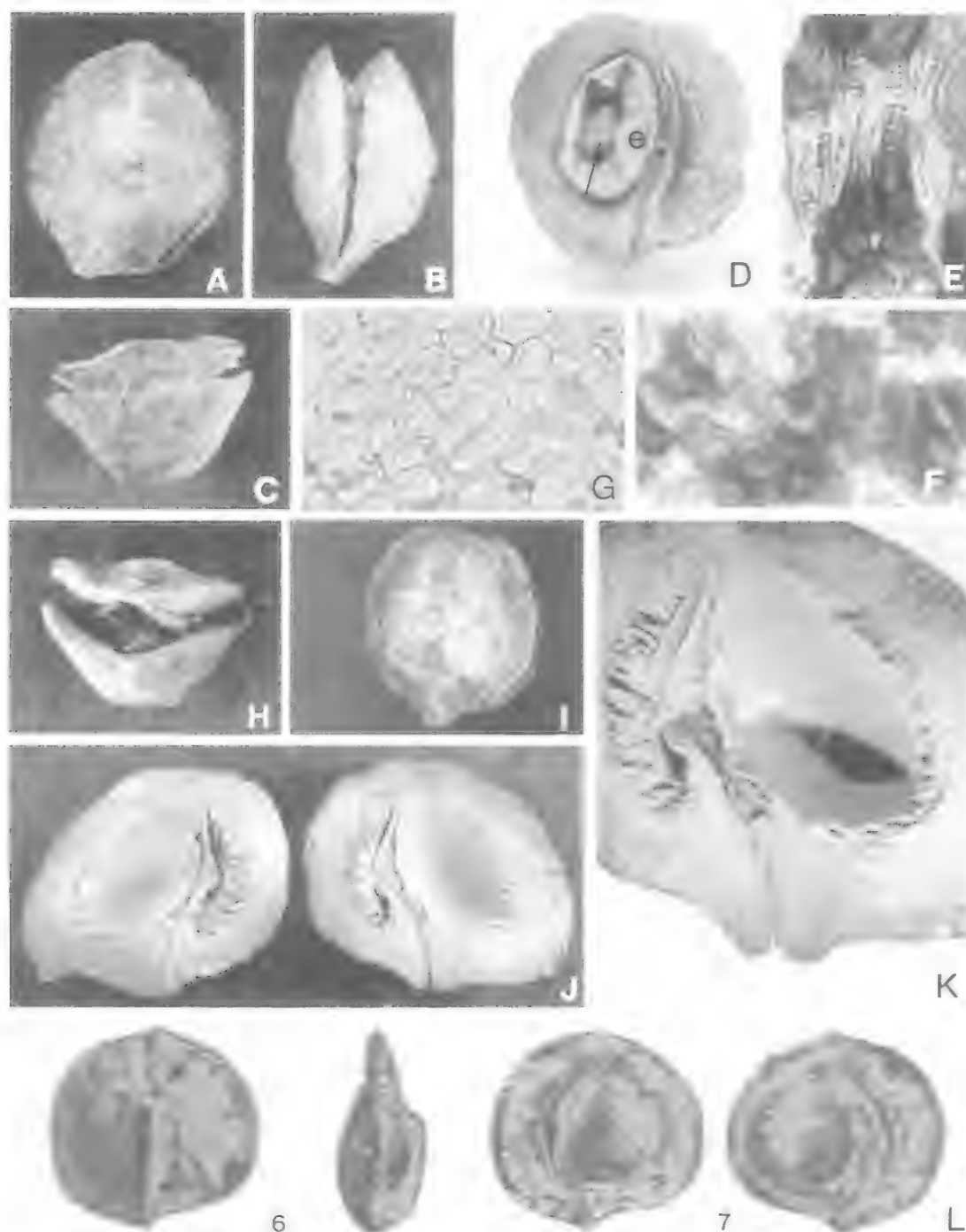


FIG. 9. *Elaeocarpus bivalve* (F. Muell.) comb. nov. fruit stones and seeds. A-C, neotype, $\times 2$, (MMF36220); A, B, lateral view; C, basal views, $\times 2$. D, internal view of segment with one sterile and one fertile locule containing seed (arrow) within endocarp (e), and compressed seedless locule, $\times 2$. E-F, outer epidermis of tegmen of seed illustrated in D showing thick-walled, pitted, bulbous sclereids, $\times 750$, $\times 250$ respectively. G, outer epidermis of testa, $\times 250$, of seed illustrated in D. H, I, fruit stone in apical and lateral views, $\times 2$. J, K, inner surfaces of the opposing valves, $\times 2$ and $\times 6$ respectively; L, specimen from Gulgong illustrated by Mueller (1878, pl. XV, figs 6, 7), $\times 1.5$.

vertical axis. The species thus differs from *E. angularis* which is 3-loculate and radially symmetrical about the vertical axis.

DISTRIBUTION. Gulgong (Home Rule, Black Lead, Forest Reef), NSW (Mueller 1877, 1879; Barnard 1881; herein); Haddon (Nintingbool, ?Crucible Co. Shaft, ~23.2m), Foster, Victoria (Mueller 1883; Deane 1925).

AGE RANGE. Early-Late Miocene.

AFFINITY. In possessing 2 locules, a smooth surface sculpture and a flanged-bilateral shape they are comparable to *E. polyandrus* A.C. Smith, which occurs on the Solomon Islands (Coode, 1978). The smooth stones of extant *E. largiflorens* C.T. White, *E. foveolatus* F. Muell., *E. ferruginifloris* C.T. White, and *E. thelmae* Hyland & Coode differ in being 3-loculate.

***Elaeocarpus brachyclinis* (F. Muell.) comb. nov.**
(Fig. 10A-L)

Penteune brachyclinis F. Muell. 1874a: 41, pl. 8, figs 1-9.

MATERIAL. LECTOTYPE (here designated): NMVP6060 (Fig. 10A-D) from the ?Early-Middle Miocene at ~47.5 m in the ?Reform Co. Shaft, at Smythe's Creek, Haddon, Victoria. Two segments of a woody inner mesocarp, originally 5-loculate, near spheroidal; vertical and lateral axes each 17mm. Segments concave externally; internally separated by the central axis, which comprises a cylinder of longitudinally orientated vascular strands extending from the base to near the apex. Locules unequal in size, one with a seed cavity and the other laterally compressed; endocarp with tangentially orientated cells. Mesocarp wall 3mm thick with pitted external sculpture. Endocarp wall thin. Seed cavity ovoid, 14-15mm long, 5-6mm wide; seed near apical, fusoid, incompletely preserved. Seed 10mm long with lateral axes of 6mm and 4mm (Mueller, 1874a, pl. 7, figs. 5,6).

DESCRIPTION. Fruit stones near spheroidal, vertical axis 15-22mm, lateral axes 15-19mm; 5-loculate and with longitudinal sutures delimiting the segments that are externally concave to straight sided; sculpture smooth to pitted. Mesocarp wall 3-4mm thick, adjacent endocarp wall thin, enclosing ovoid seed-containing or compressed locules. Seed ovoid with near apical attachment, bitegmic. Outer epidermis of testa with longitudinally arranged rectangular cells up to 80µm long and 20µm wide; inner epidermis with cuboid, thin walled cells. Outer epidermis of tegmen with elongated dumb bell-shaped lignified cells, with 18-20µm thick, pitted walls.

REMARKS. The original description was based on 'a solitary specimen'; only 2 segments of this

lectotype has been located. It is partially pyritised with adherent mineral matter. Another figured specimen (Mueller, 1874a, pl. 7, figs 7-9) is named *Penteune brachyclinis* F. Muell., but in the discussion is considered to connect *P. clarkei* and *P. brachyclinis*. This specimen, with externally concave segments, has not been located. It remains uncertain whether or not external shape of the segments is definitive for the 2 taxa as Mueller (1874a: pl. 7, fig. 2) depicted a specimen of *P. clarkei* with externally concave segments. Other specimens have externally concave (Fig. 10H) or flat (Fig. 10 F,G) surfaces.

COMPARISON. Similar to *E. clarkei*, differing in being spheroidal rather than prolate and smaller. Mueller (1874a: 41) considered 'it not improbable that they' (*P. clarkei*, *P. brachyclinis*) 'constitute merely varieties of one species'.

DISTRIBUTION. Haddon (Smythe's Creek, ?Reform Co. Shaft, ~47.5m and Nintingbool, Crucible Co. Shaft, ~23.2m), Victoria (Mueller 1874a, 1875); Gulgong (Black Lead), NSW (Barnard 1881).

AGE RANGE. ?Early- Middle to Late Miocene.

AFFINITY. Selling (1950) indicated affinity with *Elaeocarpus*. The species resembles fruit stones of extant *E. bancroftii* F. Muell. & Bailey, which, however, are rarely 5-loculate, and are larger and ovoid with segments that have convex external faces.

***Elaeocarpus cerebriformis* Rozefelds & Christophel, 1996**

Elaeocarpus sp. Christophel, 1994, fig. 2.10E.

Elaeocarpus cerebriformis Rozefelds & Christophel 1996b: 232, fig. 2a-h, 4a.

MATERIAL. HOLOTYPE (by original designation) UAY001 from late Early-Late Miocene Yallourn Formation in the Yallourn Coal Mine, Latrobe Valley, Victoria.

DESCRIPTION. Fruits prolate ellipsoidal, vertical axis 10.1-12.2mm, transverse axis 7-8.1mm; 3- or more rarely 2-loculate, with longitudinal sutures delimiting the segments, the outer surfaces of which are sculpted by prominent verrucae and rugulae, the bases of which form arches up to 2.5 × 5mm in diameter and 1mm high; crests overlie supporting columns and inter-communicating arches. Mesocarp wall 1.1-1.12 mm thick, endocarp of tangentially aligned elongated cells. Fertile locules ellipsoidal, up to 8mm long and 4mm wide. Seed

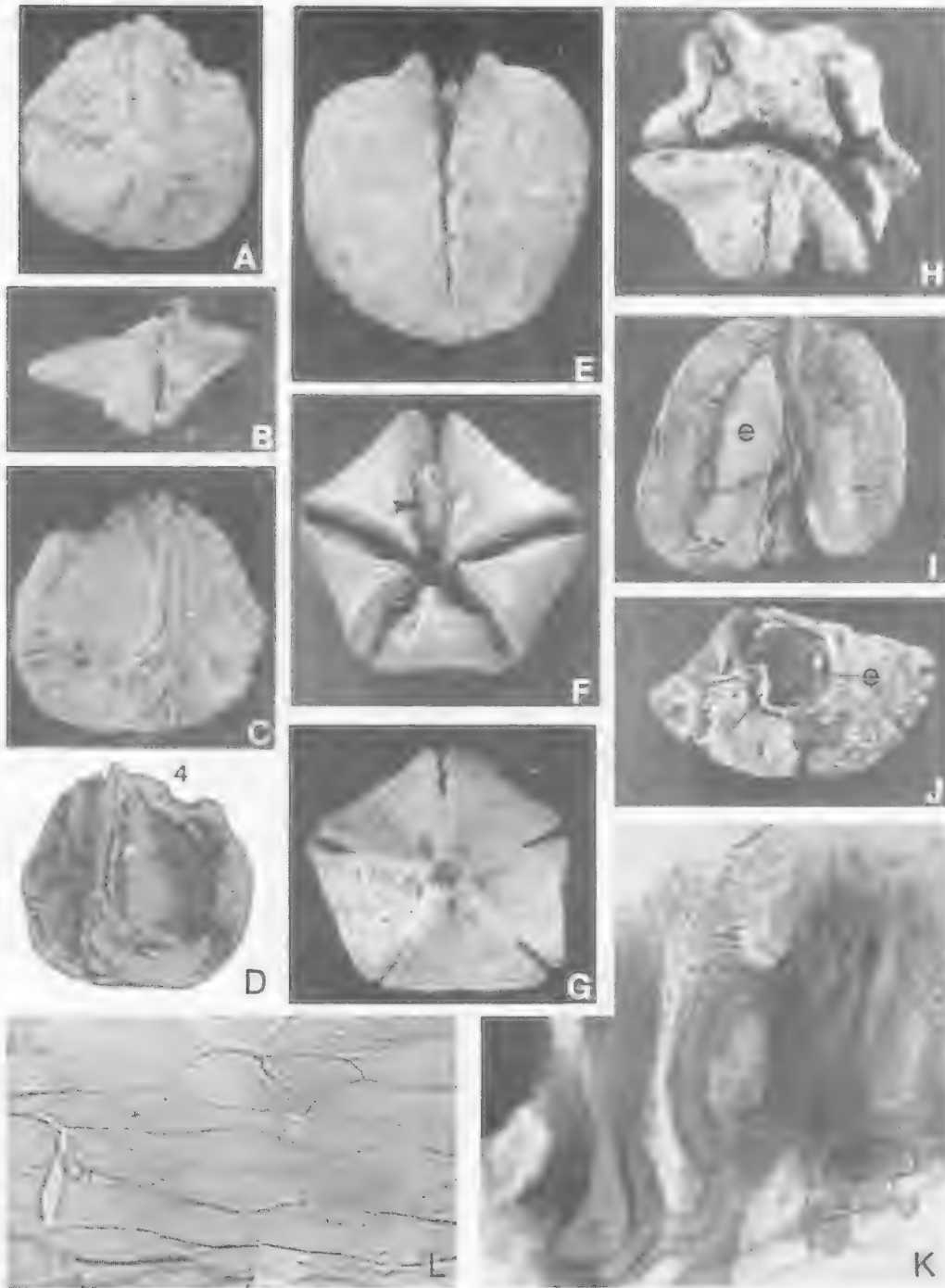


FIG. 10. *Elaeocarpus brachyclinis* (F. Muell.) comb. nov., fruit stones and seeds. A-D, lectotype, NMVP6060, $\times 2$, comprising 2 segments of an originally 5-loculate fruit stone. A, lateral view; B, apical view; C, internal surface; D, Mueller's (1874a, pl. 8, fig. 4) illustration, $\times 2$, of mirror image of specimen. E-G, lateral, apical, and basal views of a specimen containing a seed (arrow), $\times 2$. H, apical view of specimen with concave segments, $\times 2$. I, internal view of 2 segments showing endocarp (e) and seedless compressed locule, $\times 2$. J, transverse section of segment showing endocarp section (e) and seed coat (arrow) in locule, $\times 2$. K-L, seed illustrated in J; K, outer epidermis of tegmen, $\times 750$; L, outer cuticle of testa, $\times 250$.

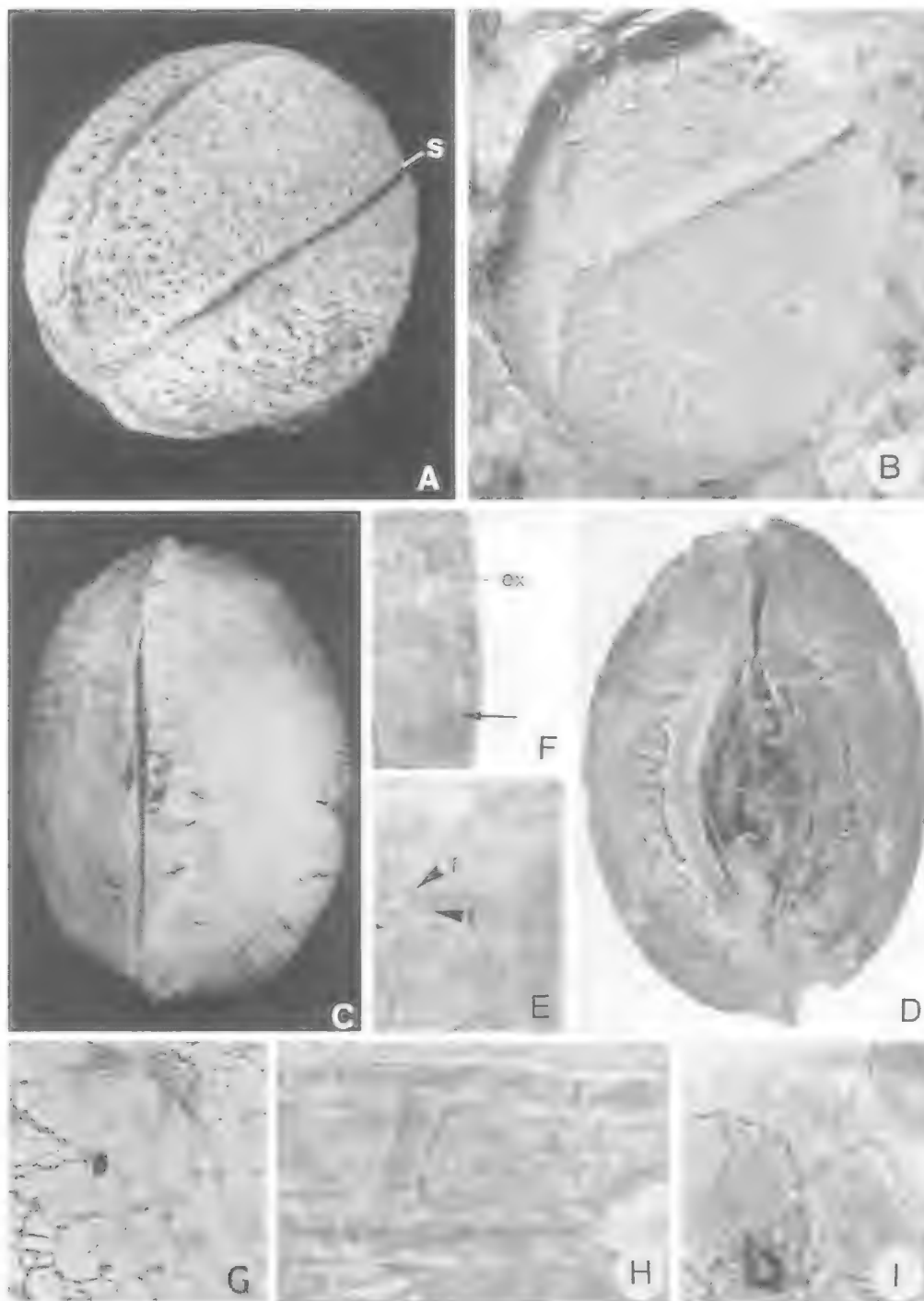


FIG. 11. *Elaeocarpus clarkei* (F. Muell.) Selling, fruit stones and seeds. A, B, oblique lateral view of fruit stone, neotype (AMF9281), $\times 2$; A, showing stalk scar and longitudinal sutures (s) of latex cast; and B, mould. C, D, lateral view of two segments of fruit, $\times 2$, with outer mesocarp and exocarp preserved; C, exterior; D, interior. E, F, detail of exocarp; E, surface showing fibre ends (f), $\times 4$; F, section showing junction between the outer and inner mesocarp (arrow), $\times 6$. G-I, tegmen; G, detail of cuboid cells, $\times 250$; H, outer epidermis of elongated sclereids with pitted walls, $\times 500$; I, spheroidal sclereids, $\times 500$.

anatropous, ellipsoidal with rounded apex. Anatomy of seed coat unknown.

COMPARISON. The 2-3 segmented fruits are prolate ellipsoidal and differ from *E. mackayi* which is spheroidal. *E. spackmaniorum* has 5 segments and is spheroidal and *E. cunningii* has smaller sculptural elements.

DISTRIBUTION AND RANGE. Yallourn, Victoria in late Early-Late Miocene sediments.

AFFINITY. Similar to *Elaeocarpus* sp. nov. 1 (Coode, 1984)/ *E.* sp. (Mossman Bluff, Henderson, 1997) from N Queensland (Rozefelds & Christophel, 1996b).

***Elaeocarpus clarkei* (F.Muell.) Selling, 1950**
(Fig. 11A-I)

Pentane clarkei F.Muell. 1874a: 41, pl. 7, figs 1-10.

Elaeocarpus clarkei (F.Muell.) Selling 1950: 558.

MATERIAL. NEOTYPE (designated Rozefelds & Christophel, 1996a: 43, pl. 1, figs A-C): AMF9281 (Fig. 10A, B, from Early Miocene at Elsmore, NSW. Mould in ironstone from which latex casts have been made. Vertical axis 31mm, transverse axes 29mm, with 5 longitudinal sutures, with punctate ornament. Internal structure of mesocarp and seeds unknown.

DESCRIPTION. Fruits with 5 or rarely 4 locules, prolate ellipsoidal; vertical axis 25-41mm long; each transverse axis 19-34mm; apex and base rounded or slightly pointed. Mesocarp segments delimited by longitudinal sutures, with convex to slightly concave outer surfaces; inner woody mesocarp with punctate sculpture, sometimes overlain by the thin, fibrous outer mesocarp and exocarp. Fruit segments separated internally by the central axis that comprises longitudinally orientated vascular strands. Inner mesocarp wall 4-6mm thick, compact. Locules enclosed by thin endocarp; with a seed cavity or compressed. Seed cavity fusiform, up to 16mm long and 10mm wide. Testa with outer epidermis composed of isodiametric cells. Tegmen multiplicative; outer epidermis comprising fibriform, lignified cells up to 200µm long, with pitted walls 20µm thick. Underlying cell layers of lignified cuboid cells and parenchyma.

REMARKS. Mueller (1874a) based the species on charcoalfied specimens from Haddon (Smythe's Creek, ?Reform Co. Shaft, ~47.5), Vic., but this material was presumed lost or destroyed by Rozefelds & Christophel (1996a) who selected a neotype from Elsmore, NSW and redefined the species. The Museum of Victoria collection contains specimens from Haddon

(Smythe's Creek, ?Reform Co. Shaft, ~47.5m) which have a thick mesocarp wall and internally about a cylinder of vascular strands that extend from the base to ~ midway to the apex. Comparable features are displayed by a specimen illustrated from Victory Mine, Orange (Fig. 11C,D).

COMPARISON. *Elaeocarpus clarkei* (F.Muell.) Selling is similar to, and may be conspecific with, *E. allportii*. *E. brachyclinis* is similar, but is smaller and spheroidal.

DISTRIBUTION. Elsmore, Bathurst, Carcoar-Orange, Orange (Forest Reefs, Victory Mine) and Gulgong (Black Lead), NSW (Mueller, 1876, 1883; Barnard, 1881; Rozefelds & Christophel, 1966a); Boola Boola, Foster (deep leads), Beechworth (Eldorado), Talbot (Victory Mine, Homebush Lead) and Haddon (Smythe's Creek, ?Reform Co. Shaft, ~47.5m), Vic. (Mueller, 1874a, 1874b, 1883; Deane, 1925; Rozefelds & Christophel, 1996a); Beaconsfield (Brandy Creek), Tasmania (Johnston, 1880a).

AGE RANGE. Oligocene-Miocene.

AFFINITY. Selling (1950) first identified the species with *Elaeocarpus*. The species is similar in size, shape and sculpture to fruits of *E. bancroftii* F.Muell. & Bail. and *E. linsmithii* Guymer, but differs in that the locule number in *E. bancroftii* is usually 4, and rarely 3 or 5, while *E. linsmithii* has 2 locules (Guymer, 1984).

***Elaeocarpus couchmanii* (F.Muell.) comb. nov.**
(Fig. 12A-G)

Pleioclinis couchmanii F.Muell. 1882: 43, pl. 19, figs 1-11.

MATERIAL. LECTOTYPE (here designated): NMVP53920 (Fig. 12A-D). Location uncertain: either from the ?Early -Middle Miocene at ~23.2m in the Crucible Shaft or ~47.5m in the Reefon Shaft at Smythe's Creek, Victoria. Six segments of 8-loculate specimen. Mesocarp woody, originally 8-loculate, and near-spheroidal (vertical axis 21.5mm, transverse axes 20.5mm). Segments with external fossulate sculpture, delimited by longitudinal sutures extending from base to apex, and internally about central hollow cylinder of vascular strands; wall 3-3.5mm thick at segment junctions. Locules developed unequally, 2 originally with a seed cavity; others compressed; endocarp wall thin. Seed cavity ellipsoidal, vertical axis 19mm, lateral axis 8mm; seed with near apical attachment, oblique ellipsoidal, 15mm long, 5mm wide.

DESCRIPTION. Fruit stones woody, near-spheroidal, 12-25mm max. diameter, usually with 8, less frequently with 6-9 locules seed bearing or compressed within thin-walled endocarps, which are enveloped by the inner mesocarp. Mesocarp segments delimited by

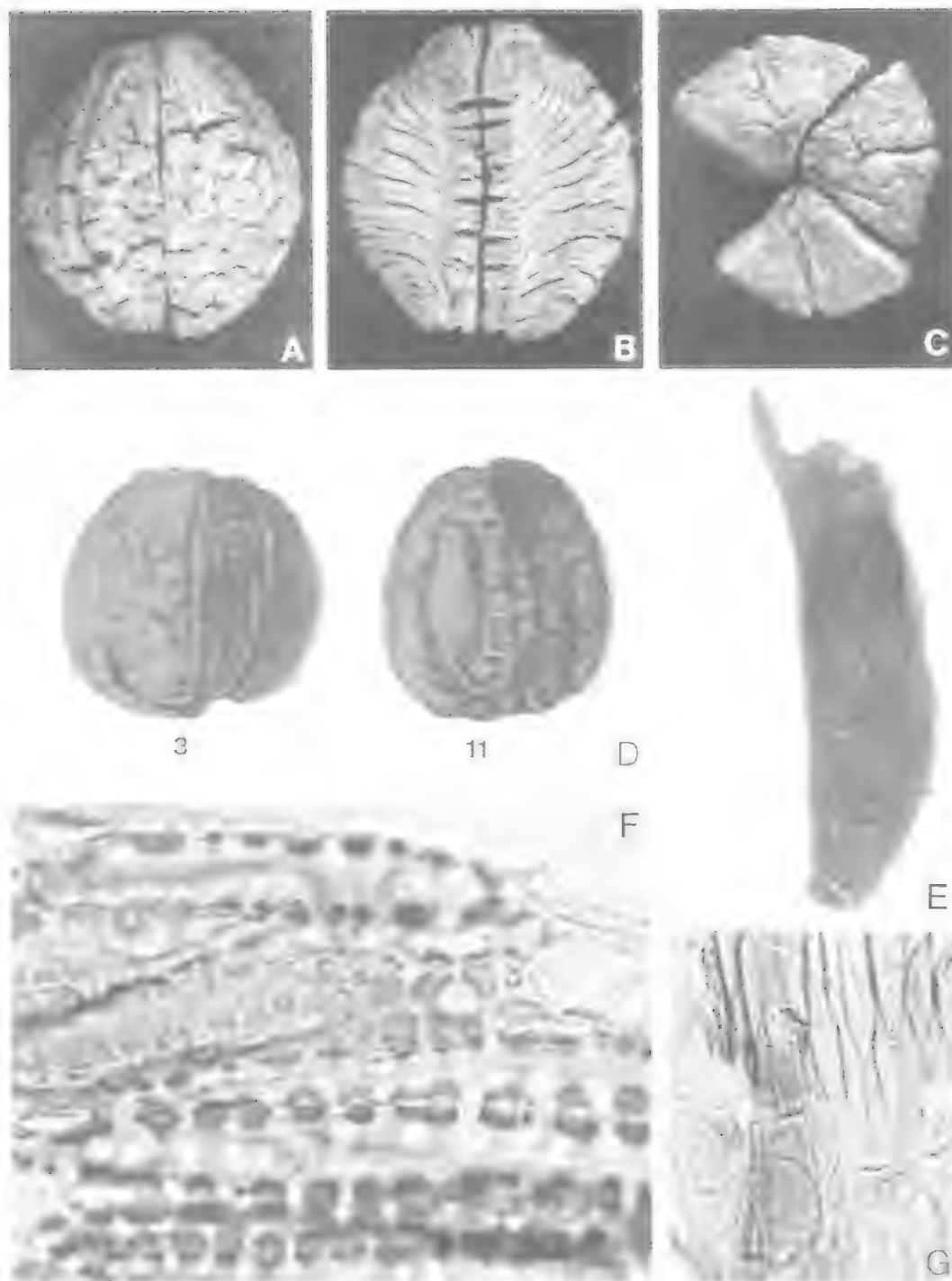


FIG. 12. *Elaeocarpus couchmanii* (F.Muell.) comb. nov., fruit stone and seeds. A-C, lectotype (NMVP53920), $\times 2$, comprising six segments of original 8-segmented fruit stone. A, lateral view; B, internal view of two fused segments; C, apical view. D, Mueller's (1882, pl. XIX, figs 3, 11) illustrations of lectotype, $\times 1.5$, but note image in his fig. 11 is reversed and seed illustrated in left hand locule has not been located. E-G, seed; E, whole specimen showing lenticular shape and apical funicle, $\times 10$; F, outer epidermis of tegmen showing thick-walled, pitted elongate sclereids, $\times 750$; G, outer cuticle of testa, $\times 250$.

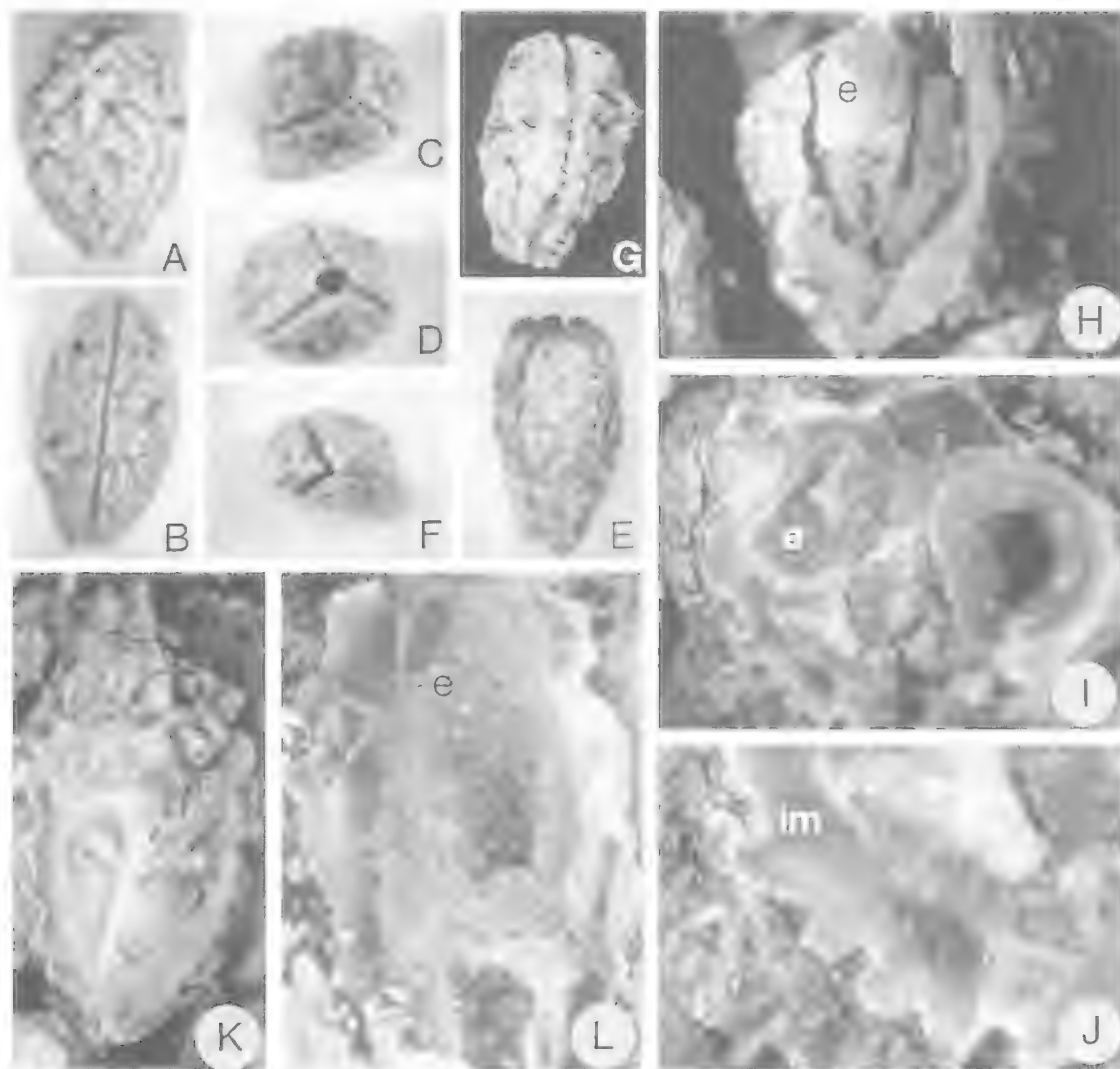


FIG. 13. *Elaeocarpus cunningii* Rozefelds, fruit stones. A-D, permineralised holotype (QMF16768, see Rozefelds, 1990, fig. 6D, right hand specimen), $\times 3$. A, B, lateral views; C, apical view; D, basal view. E-G, charcoalified specimen, $\times 3$; E, G, lateral view; and F, apical view. H, permineralised specimen in lateral view with partially exfoliated inner mesocarp showing endocarp (e) surrounding locule (see Rozefelds, 1990, fig. 6E, top left specimen), $\times 6$. I, J, transverse section of 3-loculate permineralised specimen showing sculptured inner mesocarp (im), endocarp (e), and two fully developed locules, the third compressed, $\times 10$, $\times 25$ respectively. K, permineralised specimen, oblique longitudinal section showing two locules, endocarp wall, and surface and sectional views of sculptured inner mesocarp, $\times 6$. L, longitudinal section of permineralised specimen showing crystal infilled locule, endocarp wall (e) and \sim tangential section of inner mesocarp, $\times 10$.

longitudinal sutures, with external fossulate sculpture; wall 3-4mm thick, of compact isodiametric cells with lignified walls. Endocarp with tangentially orientated elongate cells. Seed cavity ellipsoidal to fusiform; seed with near apical attachment, oblique ellipsoidal. Testa with an outer cuticle of rectangular cells; outer epidermis of tegmen of lignified, fibriform cells

(up to 150 μ m long, 2 μ m wide) with thick (4-6 μ m), pitted walls. Underlying cell layers include tannin infilled cells (up to 50 \times 100 μ m).

REMARKS. Mueller's other syntypes were not found, but material collected shortly thereafter from Nintingbool and Gulgong (Black Lead) has been examined.

COMPARISON. *E. couchmanii* differs from the 8-loculate *E. pleioclinis* in being larger and having a spheroidal, not prolate ellipsoidal, shape. Moreover, the segments of *E. pleioclinis* are externally concave and near smooth.

DISTRIBUTION. Haddon (Nintingbool, Smythe's Creek), Victoria; Gulgong (Black Lead), NSW (Mueller, 1882); Bethany, South Australia (Hossfeld, 1949).

AGE RANGE. Early-Late Miocene.

AFFINITY. Eight-loculate fruit stones with fossulate sculpture are not represented among Australian extant *Elaeocarpus*.

***Elaeocarpus cunningii* Rozefelds, 1990**
(Fig. 13A-L)

MATERIAL. HOLOTYPE (by original designation): QMF16768 from the ?Late Oligocene-Early Miocene 3km N of Glencoe Homestead, near Capella, Queensland. Mesocarp prolate ellipsoidal, vertical axis 10mm long, lateral axes each 6.5mm; 3-loculate and with 3 longitudinal, equally spaced sutures. Surface sculpted with verrucae and rugulae that have rounded crests and irregularly elongated bases up to 3mm in length.

DESCRIPTION. Mesocarp 3-4-loculate, prolate ellipsoidal, vertical axis 7-14mm, lateral axes 4.6-8.3mm. Surface sculpture verrucate-rugulate; elements with irregularly elongate bases up to 1 × 3mm, with rounded crests projecting up to 2mm from surface. Longitudinal sutures delimit 3 or rarely 4 segments. Locules unequal; 2 are with a seed cavity, the other compressed. Mesocarp wall up to 1mm thick, endocarp wall < 0.1 mm thick; mesocarp and seed anatomy unknown.

REMARKS. The description is based on permineralised specimens from the type locality and a compressed charcoalfied specimen from Picardy Station, Moranbah.

COMPARISON. *Elaeocarpus cunningii* and *E. cerebriformis* Rozefelds & Christophel are similar in size, shape, and in possessing 3 locules, but sculpture of the latter species comprises considerably larger verrucae and rugulae.

DISTRIBUTION. Glencoe near Capella, Moranbah (Picardy RDPD98MA17, 111-133m), Queensland.

AGE RANGE. Early Oligocene-?Miocene.

AFFINITY. Rozefelds & Christophel (1996b, table 2) compared the sculpture of *E. cunningii* with that of extant species including *E. reticulatus* Smith. However, the extant species has both echinae and verrucae (Fig. 7A-D). Fruit

stones of *E. holopetalus* F.Muell. have similar sculpture but are usually 2-loculate.

Elaeocarpus johnstonii
(F.Muell.) comb. nov.

Rhytidotherca johnstonii F.Muell. in Johnston 1882: 50, fig. 60-a.

Elaeocarpus bassii Ettingshausen 1883: 63, pl. 6, figs 9-12.

MATERIAL. HOLOTYPE: Specimen (Mueller in Johnston, 1882, fig. 60-a) from the Oligocene at Beaconsfield (Brandy Creek), Tasmania. This description is based on that given by Ettingshausen (1888) and the illustrations provided by him and by Johnston (1882). Mesocarp perprolate, ellipsoidal, with acute base and apex, length 26mm, axes of lateral section 7 × 13mm; 5-loculate and with 5 equal segments, each delimited externally by a suture that extends from the base to the apex. Surface with medium-high relief sculpture of irregular verrucae. Internal features not known. LECTOTYPE (here designated) of *E. bassii*: Ettingshausen 1883, pl. 6, figs 11, 12 from the Oligocene at Beaconsfield, Tasmania.

REMARKS. Mueller's (Johnston, 1882, fig. 60-a) and Ettingshausen's (1883, pl. 6, figs 11, 12) specimens from the 'Johnston collection' could not be located. The similarity of the illustrations and the remarks of Etheridge (in Ettingshausen, 1888: 63, footnote) indicate that *E. johnstonii* and *E. bassii* are based on the same specimen; accordingly the former is a senior synonym of the latter.

COMPARISON. *E. johnstonii* has 5 locules and resembles 5-locular specimens of *E. lynchii* in size and shape, but differs in having more prominent sculpture.

DISTRIBUTION. Beaconsfield (Brandy Creek), Tasmania; Ettingshausen's (1883, table II) reference to the 'Derwent District, Tasmania' is not supported by any specimen or illustration and so may be incorrect.

AGE RANGE. Oligocene-Early Miocene.

AFFINITY. With *Elaeocarpus* as suggested by Ettingshausen (1883) who made comparison with *E. angustifolius*, which, however, are spheroidal (Fig. 5).

***Elaeocarpus lynchii* (F.Muell.)**
Selling, 1950
(Fig. 14 A-O)

Rhytidotherca lynchii F.Muell. 1871b: 39, pl. IV, figs 1-8.
Elaeocarpus lynchii (F.Muell.) Selling 1950: 559.

MATERIAL. LECTOTYPE (here designated): NMVP6033, NMVP6034. (Fig. 12A-H) from the ?Early-Middle Miocene at ~25.2m in the Crucible Shaft, Nintingbool, Haddon, Victoria. Two segments of a

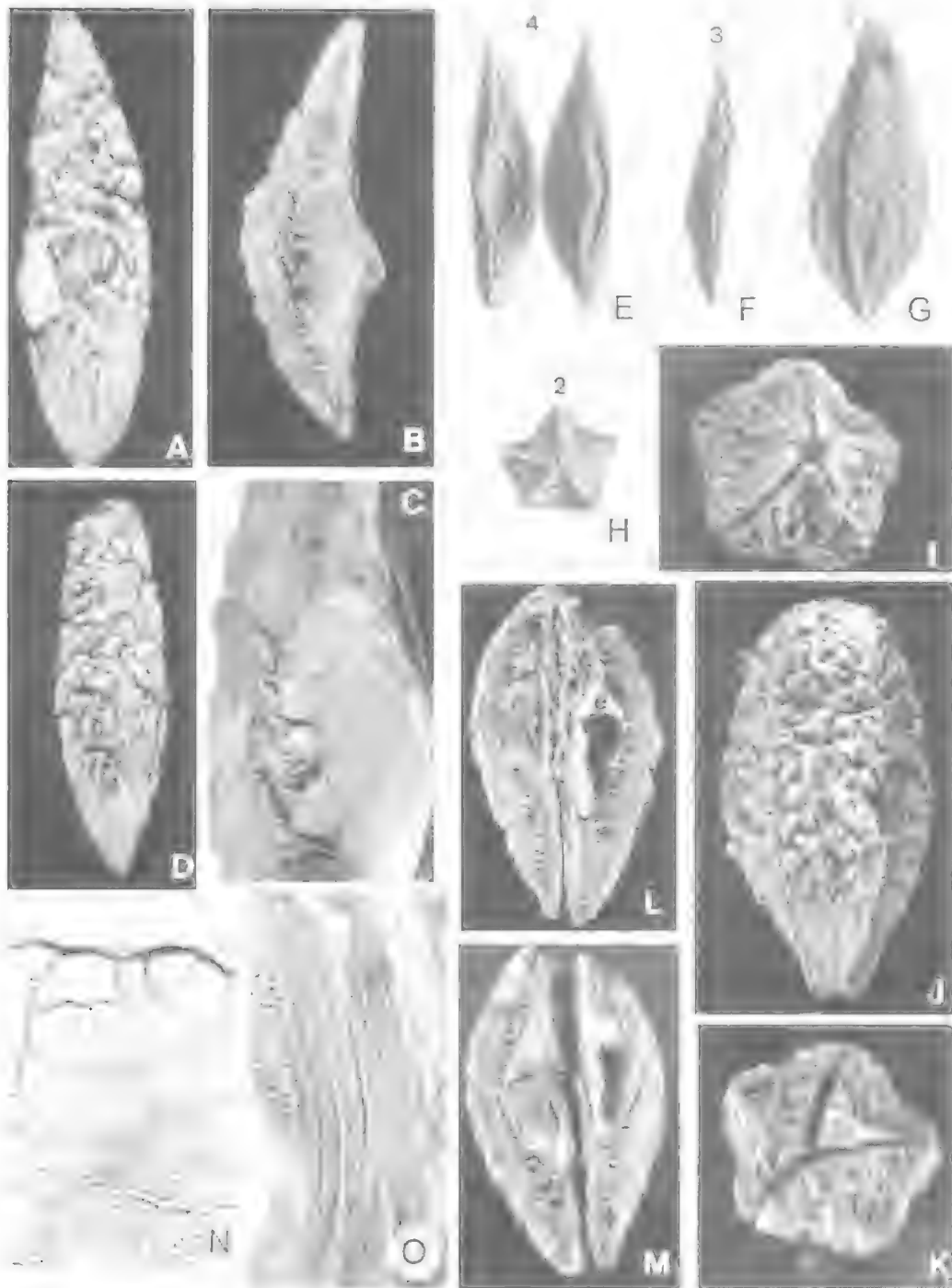


FIG. 14. *Elaeocarpus lynchii* (F. Muell.) Selling, fruit stones and seeds. A-D, lectotype comprising two segments of original 5-segmented fruit stone. A, external; and B, C, internal surfaces of one segment (NMVP6034); A, B $\times 2$, C, $\times 4$. D, external surface of other segment that is broken at apex (NMVP6035), $\times 2$. E-H, Mueller's (1871c, pl. IV, figs 1-4) illustrations of lectotype, $\times 1.2$. I-K, basal, lateral, and apical views respectively of well preserved fruit stone, $\times 2$. L, M, internal views of 4-loculate specimen showing endocarps (e) and seed cavities, $\times 2$. N-O, outer cuticle of testa showing N, hair bases and isodiametric cells, $\times 250$; and O, sclereids with thick, pitted walls from outer epidermis of tegmen, $\times 500$.

dehiscent 5-locular specimen (Mueller 1871b, pl. 4, figs 1-4). NMVP6033, representing centre segment in Mueller's fig. 1. Segment broken near distal end, with an acute base and broadening to 8mm midway between base and apex, 28 mm long; exposed locules seedless, compressed. Mesocarp wall 3.8 mm thick, with external sculpture of low (<1mm high), narrow (up to 1mm wide) sinuous rugulae and verrucae. NMVP6034, left hand segment in Mueller's fig. 4. Segment acute at base and apex, broadening to 9mm; length 34.5 mm; sculptured externally with sinuous rugulae and verrucae (<1mm high, 1mm wide). One locule with a seed cavity, the other compressed; endocarp wall thin (<0.2 mm thick), of elongated tangentially aligned cells; mesocarp wall 3.5mm thick. Seed cavity acutely ellipsoidal, longitudinal axis 10mm, transverse axis 4.5mm. Seed presumed lost or destroyed.

DESCRIPTION. Fruit stones perprolate, fusiform with an acute base and acute to rounded apex, length 28-36mm, axis of lateral section 10-17mm; 5-loculate and with 5 segments, each delimited by a longitudinal suture extending from base to apex; dehiscence loculicidal. Surface with low relief sculpture of narrow sinuous rugulae and verrucae but near smooth in abraded specimens. Locules with a seed cavity situated midway between the base and apex or compressed; seed cavity more than twice as long as wide; endocarp composed of tangentially aligned elongated cells. Seeds with near apical attachment, fusiform. Testa with outer cuticle of rectangular and polygonal cells up to 60-80µm in diameter interspersed with groups of 2-3 smaller subcircular cells representing hair bases. Tegmen with outer epidermis of fibriform, elongated sclereids (up to 120µm long, 10µm wide) with thick (5-6µm) pitted walls. Underlying layers include sheets of isodiametric parenchyma cells, some of which are tannin infilled.

COMPARISON. *Elaeocarpus lynchii* is readily distinguished from other fossil mesocarp taxa referable to *Elaeocarpus* by its perprolate shape in combination with the low relief rugulate sculptural pattern. *E. johnstonii* has a similar shape and locule number, but differs in its high relief sculpture.

DISTRIBUTION. Haddon (Ningtinbool, ?Crucible Co. Shaft, ~25.2m), Smythsedale, Foster, Victoria (Mueller, 1871b; Deane, 1925); Gulgong (Black Lead 44.5m), NSW (Barnard, 1881); Bethany, South Australia (Hosfeld, 1949).

AGE RANGE. Early-Late Miocene.

AFFINITY. Inclusion in *Elaeocarpus* was proposed by Selling (1950) which is fully

supported by features of the fruit stones, seed attachment, and seed coat. Fruit stones of extant *E. grahamii* F.Muell. are similar in shape and sculpture, but are 2-loculate.

***Elaeocarpus mackayi* (F.Muell.)**

Kirchheimer, 1935

(Fig. 15A-I)

Phymatocaryon mackayi F.Muell. 1871a: 47, pl. 2, figs 1-15.
Elaeocarpus mackayi (F.Muell.) Kirchheimer 1935: 180.

MATERIAL. LECTOTYPE (designated here) NMVP53562 (Fig. 15A, B) from ?Early-Middle Miocene at ~47.5m in Reform Co. Shaft at Smythe's Creek, Haddon, Victoria. Mesocarp subspheroidal, vertical axis 22mm, transverse axes each 24mm; with prominent sculpture of verrucae and rugulae up to 2 x 6mm in basal diameter and 1-2mm high. Mesocarp overlain in places by remains of externally smooth exocarp and outer mesocarp, which is 2mm thick; 3-loculate, with 3 external longitudinal sutures. Inner mesocarp wall 4mm thick, compact; locule wall composed of tangentially orientated elongated cells. Two locules with seed cavity, the other compressed. Seed cavity ovoid, 12mm long, 10mm wide. Seed coat bitegmic. Testa with outer cuticle of isodiametric cells 60-70µm in diameter; outer epidermis of tegmen with a lattice of elongated sclereids with thick (5-6µm), pitted, lignified walls.

DESCRIPTION. Fruit stones spheroidal to prolate-ellipsoidal with conspicuous external verrucate-baculate sculpture interrupted by 2 or more usually 3 evenly spaced longitudinal grooves. Broken specimens reveal 3 or rarely 2 locules of which 1 or 2 contain a single near apical, axial seed and the other locule(s) are sterile and compressed. Woody inner mesocarp wall 4-5mm thick, of compact isodiametric cells; endocarp of tangentially orientated elongated cells. Vertical axis of mesocarp a cylinder of strands extending from base to near the apex. External surface of mesocarp sculpted with anastomosing verrucae, bacula, and rugulae that have irregular bases up to 2.6mm in diameter and which are separated by narrow grooves up to 1mm wide and 1-2mm deep. Seed ovate (up to 10mm long, 6mm wide), attachment near apical; seed coat bitegmic.

REMARKS. The species is based on coalified specimens, 2 (including the lectotype) of which show traces of a fleshy outer mesocarp (sarcocarp of Mueller, 1871a: 47). Material examined includes the types and other specimens from the type locality, collections from Gulgong (MMF), and compressed specimens from Picardy Station, Moranbah and from near Blackwater. The Queensland specimens range

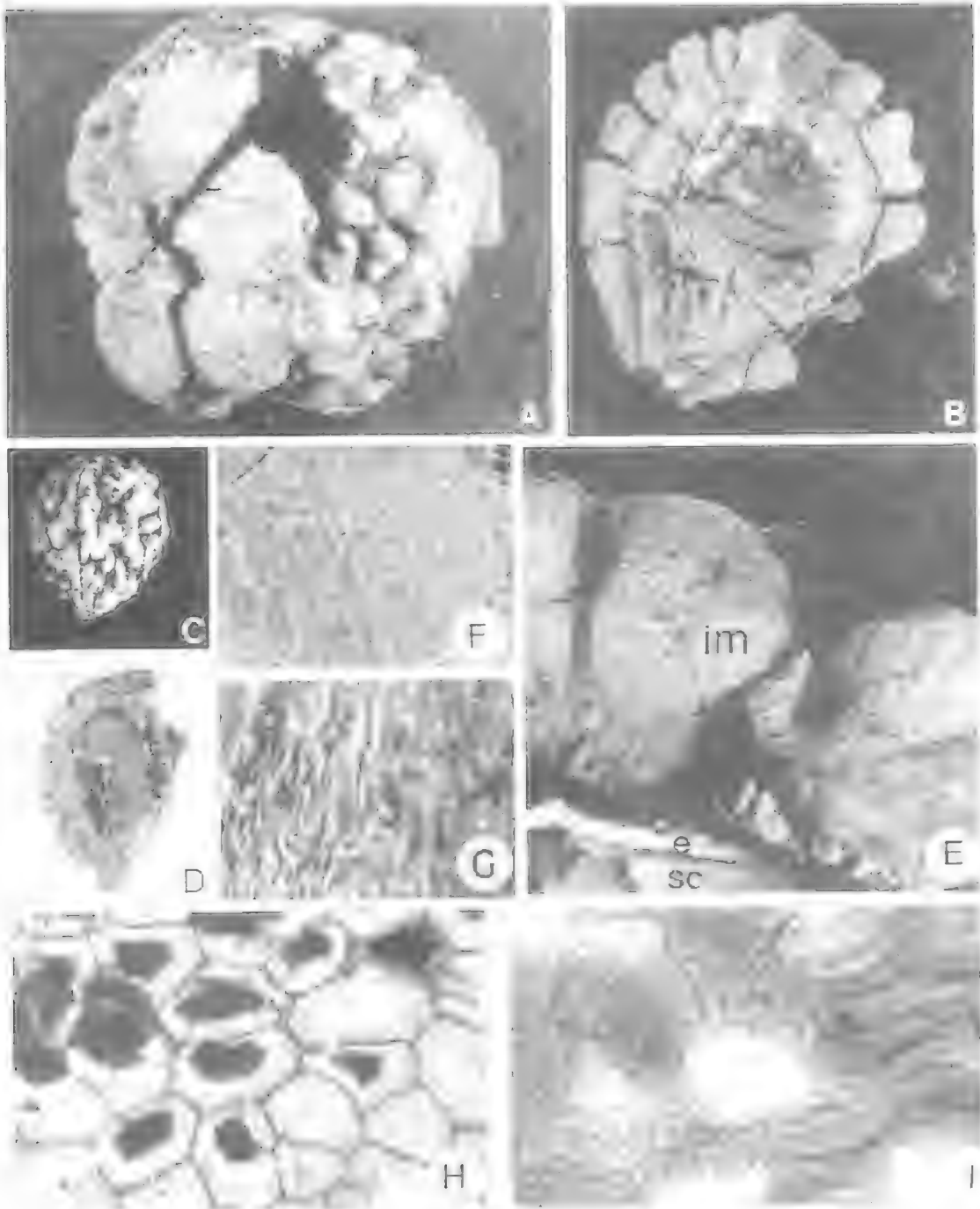


FIG. 15. *Elaeocarpus mackayi* (F.Muell.) Kirchheimer, fruits and seeds. A, B, lectotype (NMVP53562, see Mueller, 1871b, pl. II, fig. 4; Rozefelds & Christophel, in press, fig. 2A, B). A, lateral view showing preserved outer mesocarp overlying sculptured inner mesocarp; B, inner surface of segment showing seed cavity. $\times 2$. C, lateral view of small specimen. $\times 2$. D, inner surface of specimen with seed locule showing endocarp (e) and enclosed seed (sc). $\times 2.1$. E, section of inner mesocarp (im), endocarp (e) and seed coat (sc). $\times 30$. F, cell structure of inner mesocarp, $\times 200$. G, inner surface of endocarp wall of compressed locule, $\times 300$. H, outer cuticle of testa, $\times 250$. I, sclereids with thick, pitted walls from outer epidermis of tegmen of lectotype, $\times 500$.

6.25 (8.1) 10.2mm long and with transverse axes 5.52 (7.4) 9.3mm and 3.8 (4.8) 9.1mm, and approximate the size of the smaller specimens of Mueller (1871a, pl. 2, figs 8, 9, 13-15).

COMPARISON. *E. mackayii* and *E. spackmaniorum* are similar in their sculptural attributes and 3-loculate specimens of the latter may imply intergradation of the species. *E. mackayii* differs from *E. cerebriiformis* in having a near spheroidal shape. *E. cunningii* is prolate-ellipsoidal and has sculpture of smaller-based and lower elements.

DISTRIBUTION. Haddon (Symthe's Creek, Reform Co. Shalt, ~47.5m), Beechworth (Eldorado), Tanjil, Victoria (Mueller, 1871a, 1874b; Deane, 1925); Dubbo, Orange (Victory Mine, Forest Reefs), Gulgong (Black Lead 146 ft.), NSW (Mueller, 1874b, Barnard, 1881, Rozefelds & Christophel, in press); Launceston, Tasmania (Mueller, 1883); Bethany, South Australia (Hossfeld, 1949). Recorded herein from near Moranbah (Picardy RDPD98MA17, 111-133m, Picardy RDPD98MA21, 123-133m) and South Blackwater (Hole R8736, 82m).

AGE RANGE. Early Oligocene-Miocene.

AFFINITY. With *Elaeocarpus* as recognised by Deane (1925), Kirchheimer (1935), Selling (1950) and Rozefelds & Christophel, who note congruence with fruit stones of *E. angustifolius*, but these differ in being 5- or rarely 4-loculate.

***Elaeocarpus muelleri* Ettingsh., 1886**

Elaeocarpus muelleri Ettingsh. 1886: 157, pl. 14, figs 4, 5.

MATERIAL. LECTOTYPE (here designated): Ettingsh. 1886, pl. 14, fig. 4; specimen lost according to records of the Australian Museum; from Early Miocene at Newstead near Elsmore, NSW. The description follows that of Ettingshausen. Mesocarp preserved in ironstone, prolate, 5-loculate; external surface with 5 longitudinal sutures and a sculpture of wrinkles.

REMARKS. The species was based on a mesocarp and a leaf from a different locality and horizon; is here restricted to the mesocarp.

COMPARISON. Ettingshausen (1886) indicated that fruit stones of *E. muelleri* differ from those of his *E. bassii*, which is perprolate and has less prominent sutures.

DISTRIBUTION AND AGE RANGE. Type locality; Early Miocene.

AFFINITY. Ettingshausen (1886) suggested close similarity to fruit stones of *E. angustifolius* Blume.

***Elaeocarpus peterii* Rozefelds & Christophel, 1996 (Fig. 16A-D)**

Elaeocarpus peterii Rozefelds & Christophel 1996a: 45, pl. 3, figs A,C,E,G,I.

MATERIAL. HOLOTYPE (by monotypy) QMF18088 (Fig. 16A-D) from ?Late Oligocene-Early Miocene 3km N of Glencoe Homestead, near Capella, Queensland. Mesocarp, oblate ellipsoidal with a broad base, rounded apex, and 6 longitudinal ridges separated by concave surfaces that extend from base to apex; vertical axis 23mm, transverse section stellate, transverse axes each 27mm. Stalk scar circular, 4mm in diameter. Sutures are embedded in the longitudinal ridges. Preserved mesocarp wall 3-5mm in section comprising a thick outer layer and a thin (<1mm) inner layer (?endocarp). Trace of latter layer indicating 2 compressed locules adjacent to central cavity (?fertile locule). External surface with small pits.

REMARKS. The species externally resembles fruit stones of extant *E. stellaris* and undescribed *Elaeocarpus* sp. from N Queensland (Rozefelds, pers comm.) in shape and longitudinal sutures embedded in the projecting ridges. The hollow central region implied to Rozefelds & Christophel (1996a: 45) that 'replacement of internal mesocarp structure has not occurred'. This central region is partially infilled and surrounded by a layered wall, the outer broad layer of which may represent the mesocarp and the narrow inner layer the endocarp. Moreover, the trace of the endocarp implies 2 compressed locules adjacent to the main central cavity, which may represent the seed cavity. The banding represented in the inner mesocarp (Fig. 16C) is due to layering in the opaline silica and is unrelated to original structures.

COMPARISON. External morphology resembles that of the charcoallified specimens assigned to *E. rozefeldsii* sp. nov., and should it be shown that internal organisation of the two taxa be comparable, the latter species will be a junior synonym of *E. peterii*.

DISTRIBUTION AND AGE RANGE. Known only from the type locality in ?Late Oligocene-Early Miocene sediments.

AFFINITY. Rozefelds & Christophel (1996a) considered *E. peterii* similar to fruit stones of extant *E. stellaris*.

***Elaeocarpus pleioclinis* (F.Muell.) comb. nov. (Fig. 17A-M)**

Rhytidotecha pleioclinis F.Muell. 1873: 42, pl. 6, figs.1-4.
Pleioclinis shepherdii F.Muell. 1882: 43.

MATERIAL. LECTOTYPE (here designated): NMVP53747 two complete segments as originally illustrated (Mueller, 1873: pl. 6, fig. 3,4) and one broken segment of a 8-locular mesocarp (Fig. 17A-D) from ?Early-Middle Miocene at ~23.2m in Crucible Co Shaft,

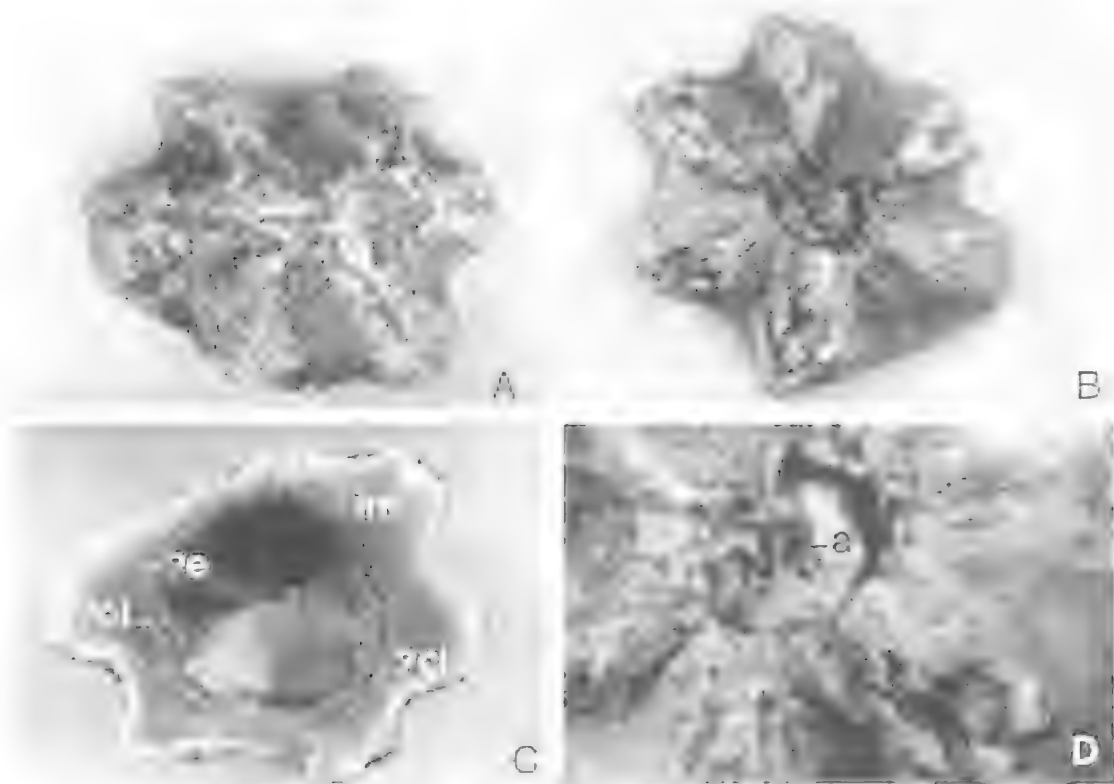


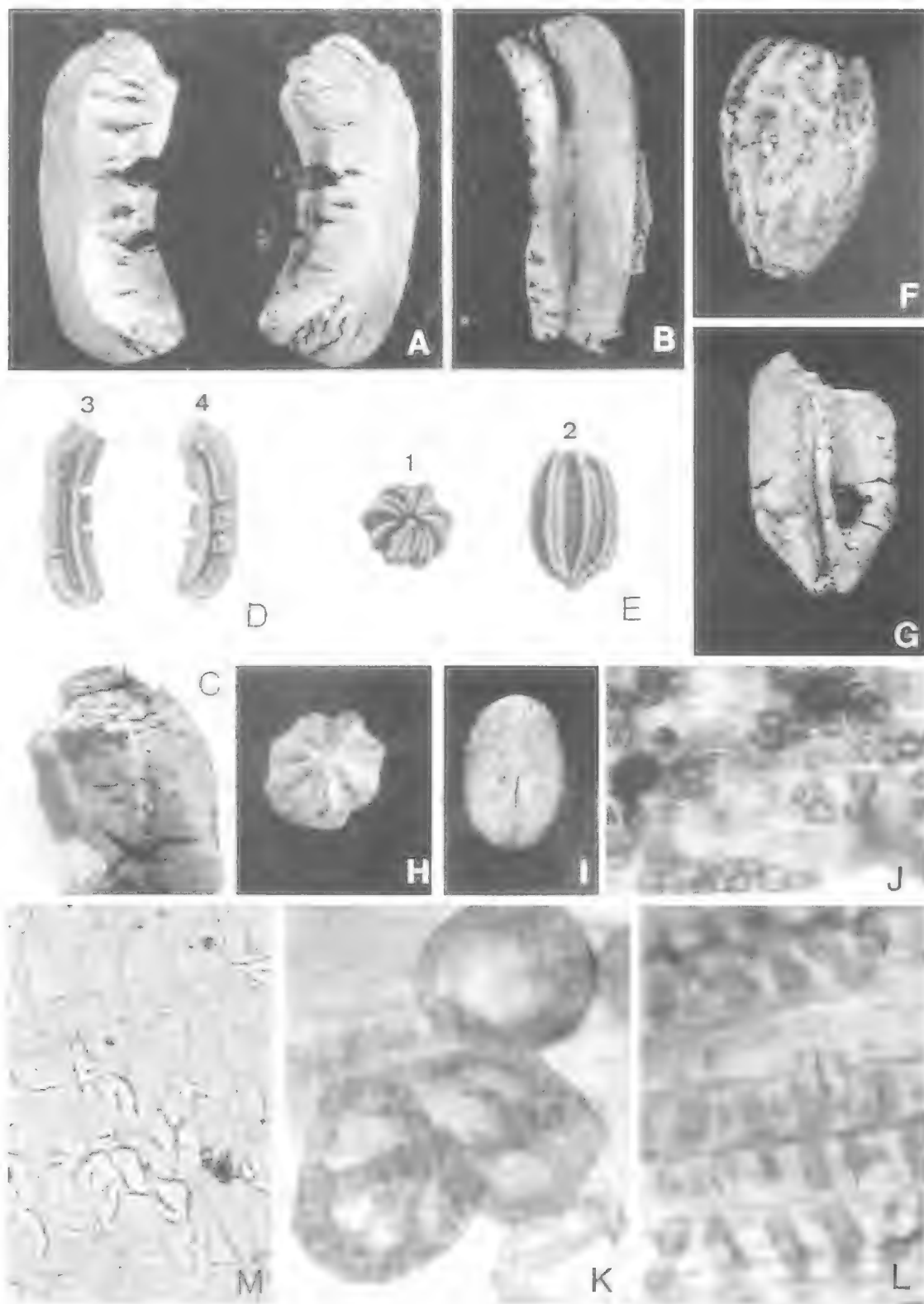
FIG. 16. *Elaeocarpus peterii* Rozefelds & Christophel fruit stone. A-C, permineralised fruit stone, holotype (QMF18088, see Rozefelds & Christophel, 1996a, pl. 3, figs A,C,E,G,I), $\times 2$. A, apical view; B, basal view; and C, transverse section, showing broad banded inner mesocarp (im) probable thin endocarp (?e) and possible compressed locules (?cl). D, detail of base showing vascular tissue in axial canal (a), $\times 4$.

Nintingbool, Haddon, Victoria. Segments 16mm long, with a concave, unsculptured outer surface 5mm wide; internally each segment of 2 half locules one of which has a seed cavity and the other compressed. Mesocarp wall 3mm thick, composed of compact isodiametric cells, but with secondarily radial fractures; endocarp <1mm thick, composed of tangentially aligned cells. Seed cavities up to 10mm long \times 2mm wide; seeds not observed.

DESCRIPTION. Fruit stones prolate ellipsoidal, swelling from an acute base to a broadly rounded apex, length 8.1–13.5mm, transverse axes each 6–9mm; 8-loculate and with 8 externally concave segments, each delimited by a longitudinal suture that extends from base to apex. Surface near smooth or irregularly pitted in abraded specimens; mesocarp wall up to 3mm thick, composed of compact isodiametric cells. Locules enclosed by endocarps about central axis of a cylinder of vertically aligned vascular strands. Endocarp of tangentially orientated elongated cells. Fertile locules with a seed cavity, others compressed. Seed cavity and near apical seed fusiform, at least

twice as long as wide; seed coat bitegmic. Testa with outer cuticle of rectangular cells up to 50 μ m long and 20 μ m wide; outer epidermis of tegmen of linearly arranged longitudinal sclereids having thick (4 μ m) pitted walls overlying a layer of subspherical (40–50 μ m in diameter) sclereids with similarly thick, pitted walls. Other tegmen tissue parenchymatous layers of thin walled isodiametric cells (up to 20 μ m in diameter).

REMARKS. Mueller (1873) based the species on charcoalfied specimens, and noted that it comprised a smaller and a larger form. The lectotype is larger than, but otherwise comparable to, the other specimen (Mueller, 1873, pl. 6, figs 1,2) and some other specimens (NMVP53741). In allocating the species to *Rhyditheca* Mueller (1873: 42) noted that it may 'require generic separation' and later (Mueller, 1882: 43) moved it to *Pleioclinis* introducing the replacement *P. shepherdi* which becomes an objective synonym.



COMPARISON. *E. pleioclinis* possesses 8-loculate fruits, a condition thus far only known among fossil *Elaeocarpus* in *E. couchmanii*. The latter species differs in its larger size, spheroidal shape, and fossulate sculpture.

DISTRIBUTION. Known only from the type locality.

AFFINITY. The organisation of the fruit stone and anatomy of the seed coat are consistent with *Elaeocarpus*. However, extant Australian and New Zealand species with smooth or near smooth sculpture are 3-loculate.

***Elaeocarpus rozefeldsii* sp. nov.**
(Fig. 18A-F)

ETYMOLOGY. For Andrew Rozefelds in appreciation of his helpful discussions and for providing literature.

MATERIAL. HOLOTYPE: QMF50123 (Fig. 18A,C) from Early-Late Oligocene at 82m in South Blackwater Coal Pty Ltd Hole R8736. Near Blackwater, Queensland. Longitudinally ribbed, 7-loculate inner mesocarp, ellipsoidal; compressed obliquely to the vertical plane with vertical axis 18mm, stellate in lateral section, with axes of 18mm and 13mm; base and apex broadly rounded. Seven longitudinal ridges embedded with sutures extend from near base to apex, delimiting segments with externally concave, near smooth faces. Preserved mesocarp wall 2-3mm thick.

DESCRIPTION (7 specimens). Fruit stones woody, 5-7-loculate, ellipsoidal, laterally compressed, stellate in lateral view; vertical axis 14 (16.6) 18mm, lateral section with axes of 14 (16.5) 18mm and 9 (11.8) 13.5mm. Base and apex broadly rounded, the base with a near circular cavity; longitudinal ridges with sutures embedded in their crests extend from base to apex and delimit mesocarp segments that are externally concave and without sculpture. One or more of the locules with a seed cavity, the others compressed; seed cavity up to 6mm long and 5mm wide. Inner mesocarp wall 2-3.5mm thick, anatomy not determined; endocarp <0.5mm thick; internally locules about hollow axis. Seed cavity ovoid, acute apically, broadening to base, 9-10µm long, 4-5µm wide. Seed fragmented, anatomy of seed coat not determined.

REMARKS. Charcoalified specimens (QMF50123-50126, QMF51079-51081) included within the species are laterally compressed and have been subjected to abrasion and thermal alteration. Nevertheless their characters (5-7 locules, one or more of which has a seed cavity, loculicidal dehiscence and externally concave segments) support assignment to *Elaeocarpus*.

COMPARISON. *E. rozefeldsii* may be synonymous with *E. peterii* should the latter species be shown to possess 5-7 locules. In possessing externally concave, near-smooth segments, *E. rozefeldsii* is similar to *E. pleioclinis*, but differs in its larger size and fewer locules.

DISTRIBUTION AND AGE. Known only from the type locality (Early-Late Oligocene).

AFFINITY. With *Elaeocarpus*, possibly *E. stellaris* L.S.Smith, fruits of which are typically 5-loculate, rarely 7-loculate (Rozefelds & Christophel, 1996a).

***Elaeocarpus spackmaniorum* Rozefelds, 1990**
(Figs 19A-M, 20A-F)

MATERIAL. HOLOTYPE (by original designation) QMF15440 (Fig. 19A-C) from ?Late Oligocene-Early Miocene 3km N of Glencoe Homestead, near Capella, Queensland. Permineralised 5-loculate inner mesocarp, spheroidal, vertical and lateral axes 12.5mm. Five longitudinal sutures extend from base to apex and delimit 5 segments that have prominent sculpture of verrucae and rugulae up to 1.3mm in basal diameter and 0.5-1mm high.

DESCRIPTION. Fruit stones spheroidal, vertical and transverse axes 8-13.5mm with 5 or, more rarely, 3-4 locules and segments, the latter delimited by longitudinal sutures. Inner mesocarp wall 1.2-2mm thick, composed of compact isodiametric cells; sculpted externally with verrucae, bacula, and rugulae; sculptural elements up to 1mm high, 1mm wide and 2-4mm long. Locules equally developed or the seedless locules compressed; thin endocarp with tangentially oriented elongate cells and hollow central axis represented in sectioned specimens. Seed cavity ovoid,

FIG. 17. *Elaeocarpus pleioclinis* (F.Muell.) comb. nov., fruit stones and seeds. A-D, lectotype comprising two segments of original 8-locular fruit stone (NMVP53747, see Mueller, 1873, pl. VI, figs 3, 4). A, lateral view of two segments showing inner and outer surfaces, $\times 3$. B, external surface of segment on right in A, $\times 3$. C, detail of apical part of segment on right in A, $\times 4$. D, Mueller's (1873, pl. VI, figs 3, 4) illustration of lectotype, $\times 1.5$; E, Mueller's (1873, pl. IV, figs 1, 2) illustration of another specimen in apical and lateral view, $\times 1.5$. F, G, lateral view of F, external and G, interior surface, $\times 3$. H, apical, $\times 3$, and I, lateral, $\times 2$, views of specimen. J, spherical sclereids with pitted walls underlying elongate sclereids of outer epidermis of tegmen, $\times 250$. K, detail of spherical sclereids, $\times 750$. L, detail of elongated sclereids with thickened, pitted walls forming outer epidermis of tegmen, $\times 750$. M, outer cuticle of testa, $\times 750$.

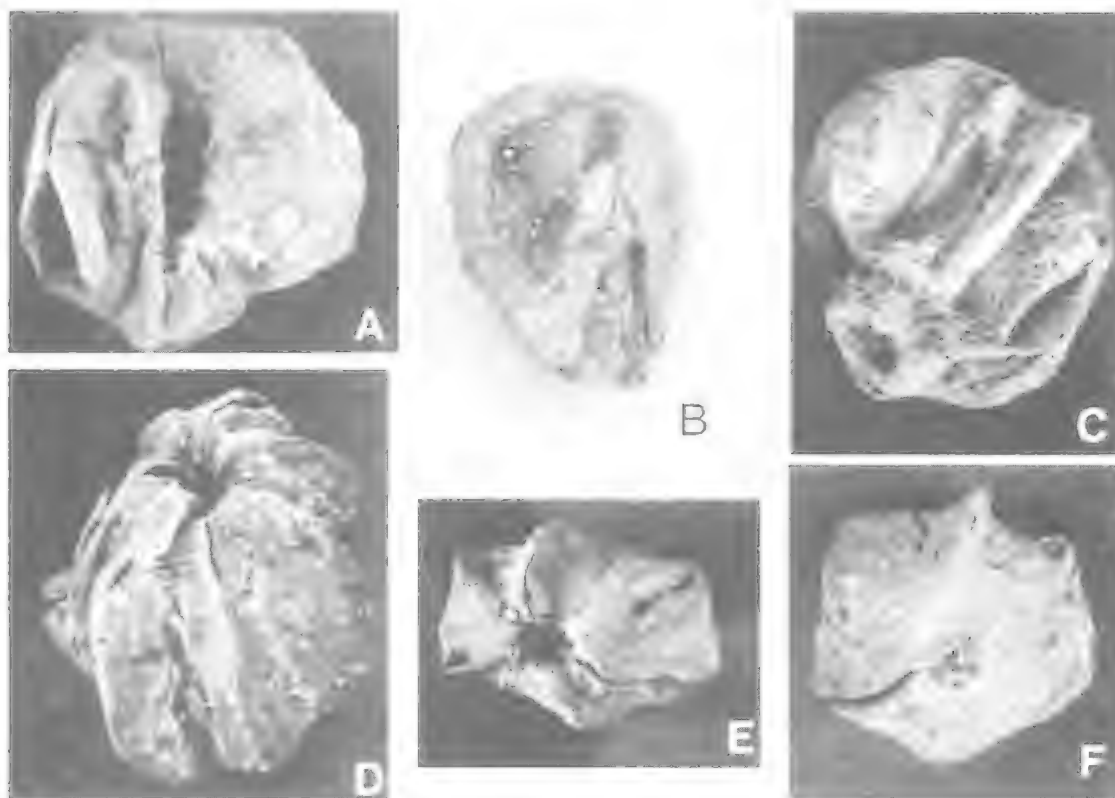


FIG. 18. *Elaeocarpus rozefeldsii* sp. nov. fruit stones. A, C', holotype, $\times 2$, QMF50123 showing externally concave segments and seed cavity; A, lateral view; C, oblique view. B, internal view of segment, $\times 2$, showing seed cavity. D, oblique apical view of larger specimen, $\times 2$. E-F, another specimen, $\times 2$; E, apical view; F, basal view.

up to 9mm long, 4mm wide. Seed with near apical attachment, ovoid; seed coat bitegmic.

REMARKS. In their amplified description of the species Rozefelds & Christophel (in press) note an exocarp and outer mesocarp on one specimen, thus corroborating identity with *Elaeocarpus*; fibre bases occur on the outer surface of the inner mesocarp in some specimens (Fig. 19J). A permineralised specimen transversely sectioned displays equally developed locules, but another specimen from the same locality shows a single seed bearing locule with the other locules compressed (Fig. 19K-M).

COMPARISON. *E. mackayi* is spheroidal with similar sculptural attributes and intergrades with 3-loculate specimens of *E. spackmaniorum*. *E. couchmanii* has a greater number (7-9) of locules and has fossulate sculpture. *E. trachyclinis* has rugulate sculpture and is considerably larger (~30mm in diameter).

DISTRIBUTION. Glencoe near Capella, Picardy Station near Moranbah, Hole RDPD998MA 17at 111-133m, Qld; Guildford, Vic. (Rozefelds, 1990; Rozefelds & Christophel, in press).

AGE RANGE. Oligocene-Early Miocene.

AFFINITY. Resemblance to *E. angustifolius* Blume was emphasised by Rozefelds (1990) and Rozefelds & Christophel (1996a, in press), but fruit stones of extant species are usually larger.

***Elaeocarpus trachyclinis* (F.Muell.) Selling, 1950**
(Fig. 21A-I)

Penteme trachyclinis F.Muell. 1874a: 41, pl.8, figs.10-17.
Elaeocarpus trachyclinis (F.Muell.) Selling 1950: 559.

MATERIAL. **LECTOTYPE** (here designated): NMV53758 (Mueller 1874a, pl. 8, fig. 10, 11; Fig. 21D-G) from ?Early-Middle Miocene at ~47.5m in Reform Co Shafy, Smythe's Ck, Haddon, Victoria. Two fragmented segments of a partially pyritised woody inner mesocarp that was originally 5-loculate and near spheroidal, vertical axis 30mm and the transverse axes 32mm. Segments

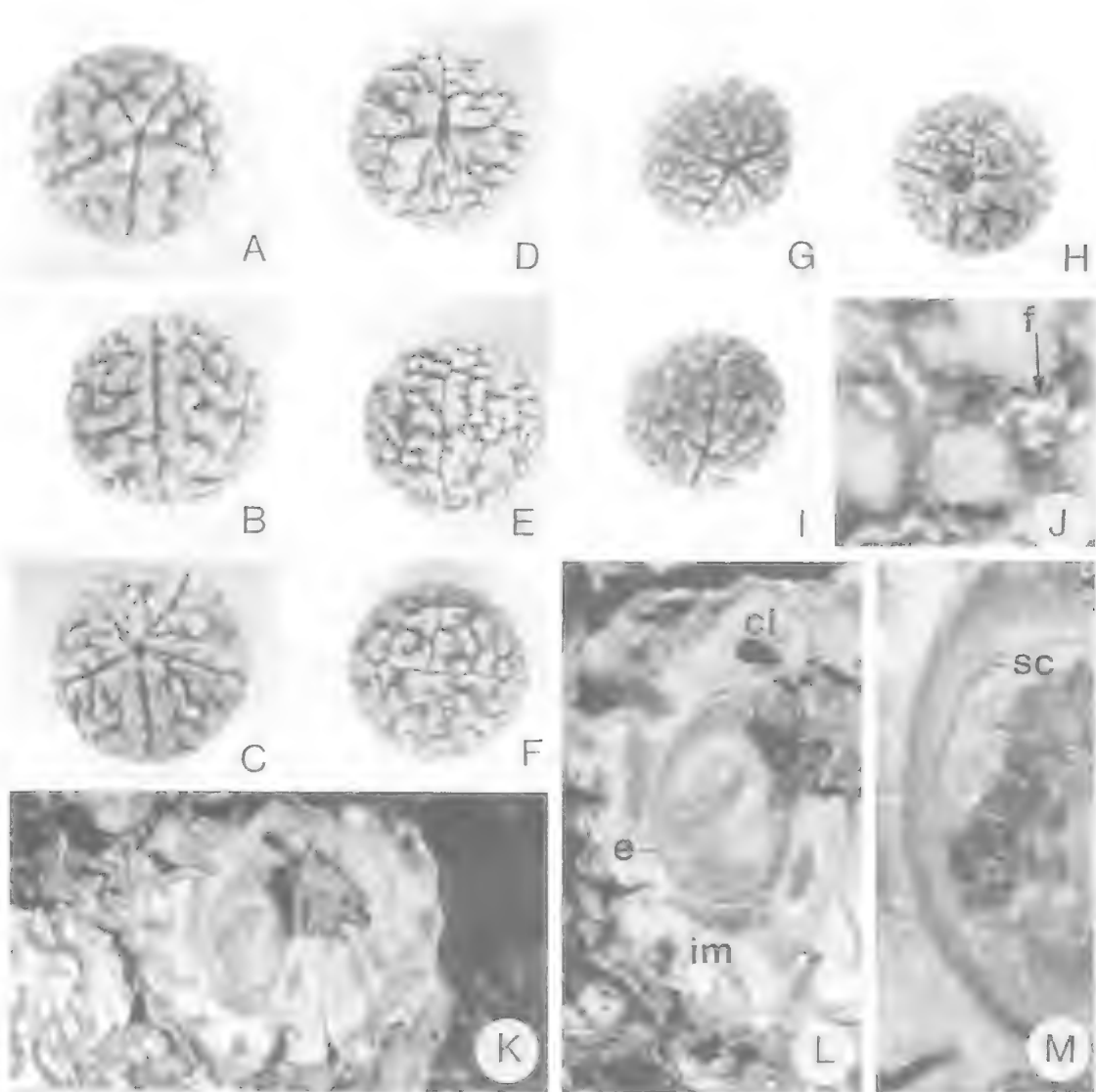


FIG. 19. *Elaeocarpus spackmaniorum* Rozefelds, permineralised fruit stones. A-C, holotype (QMF15440, see Rozefelds, 1990, fig. 4 A,B), $\times 2$; A, apical view; B, lateral view; C, basal view. D-F, paratype (QMF15442, see Rozefelds, 1990, fig. 5 A,B), $\times 2$; D, apical view; E, lateral view; F, basal view. G-I, paratype (QMF15444, see Rozefelds, 1990, fig. 4G), $\times 2$; G, apical view; H, basal view; I, lateral view. J, surface detail of inner mesocarp and fibres (f) preserved on surface, $\times 16$. K-M, oblique transverse section of fruit stone with one seed-bearing locule and two compressed locules (cl); note endocarp wall (e), seed coat (sc) and irregularly crested sculptural elements on the surface of the inner mesocarp; J, $\times 6$, K, $\times 4$, L-M $\times 16$.

convex externally, with rugulate sculpture. One locule with an ovoid seed cavity 5mm wide and 14mm long, the other compressed; mesocarp wall 5mm thick, with many transverse cracks; endocarp not preserved.

DESCRIPTION. Fruit stones spheroidal or ellipsoidal when compressed, the vertical axis 32-36mm and transverse axes 25-35mm; sculpted externally by rugulae, with 5 evenly

spaced longitudinal sutures. Fruits 5-loculate, 1 or more containing a single near apical seed, other locules sterile and compressed. Mesocarp 5-6mm thick, sculpted with rugulae (1mm wide, up to 6mm long) orientated near parallel to the vertical axis in well-preserved material; in abraded specimens sculpture much reduced:

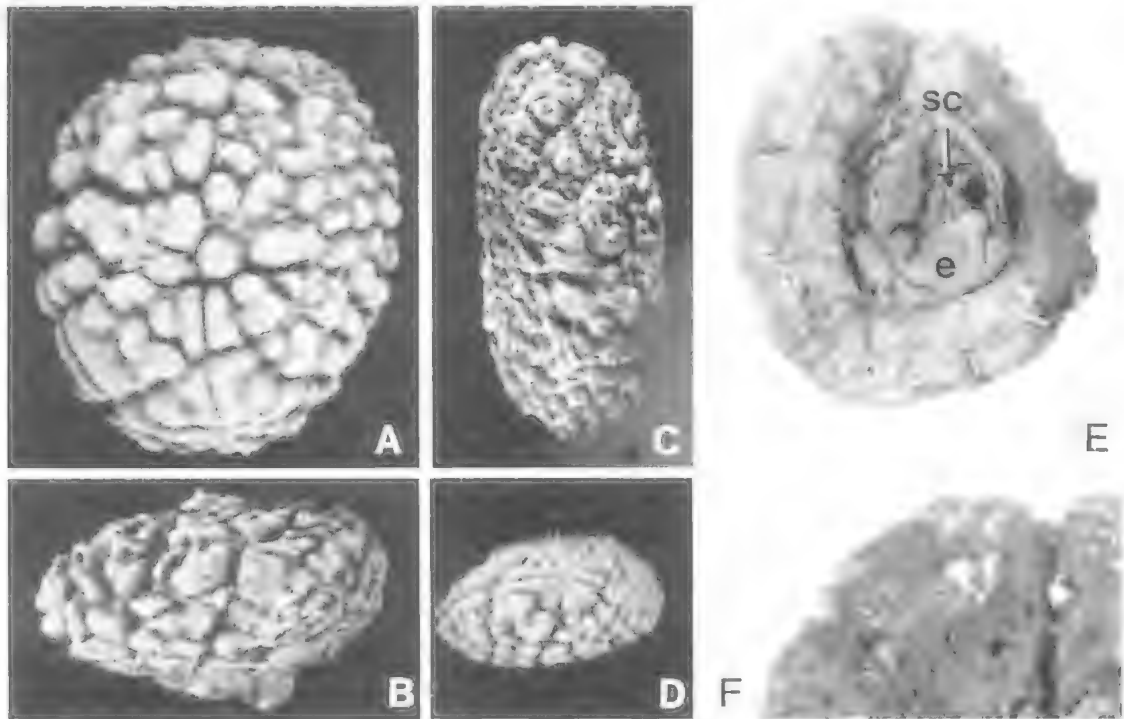


FIG. 20. *Elaeocarpus spackmaniorum* Rozefelds, charcoalfied fruit stones and seeds. A-D, compressed specimen, $\times 2$; A, C, lateral views; B, D, apical views. E, F, internal surface of segment; E, seed-bearing locule with endocarp (e) and seed coat (sc), $\times 4$; F, detail of inner mesocarp $\times 10$.

Endocarp wall thin, enclosing ovoid locules with seed cavity 18mm long, 12mm wide.

REMARKS. The species was based on segments of 2 charcoalfied, partially pyritised specimens.

COMPARISON. Similar in sculpture to *E. lynchii* which however is perprolate.

DISTRIBUTION. Haddon (Smythe's Creek, Reform Co Shaft, ~47.5m; Nintingbool, Crucible Co. Shaft, 23.2m), Beechworth (Eldorado), Victoria (Mueller 1874b, Mueller 1875); Risdon, Tasmania (Johnston, 1882); Bethany, South Australia (Hosfeld, 1949).

AGE RANGE. Oligocene-Miocene.

TAXON QUESTIONABLY ATTRIBUTABLE TO *ELAEOCARPUS*

Rhytidotheca major Deane, 1925

Rhytidotheca major Deane, 1925: 491, pl. LX, fig. 12 (nomen nudum).

REMARKS. The single specimen from Foster, Victoria figured by Deane (1925: 491) is said to be 'portion of a valve of a fruit like a large *Rhytidotheca*', but no description was provided

and the name is thus a nomen nudum (Greuter et al., 1994, Art. 32).

FOSSIL FRUIT TYPES OF *ELAEOCARPUS* AND THEIR DISTRIBUTION IN TIME AND SPACE

Fossil fruit stones of *Elaeocarpus* display a greater morphological range than that detailed for extant Australian and New Zealand species. However, it has been demonstrated that several of the fossil taxa have near congruence with fruit stones of extant Australian species. For example, fossil fruit stones *E. cerebriformis* differ only in size from those of *Elaeocarpus* sp.1 (Coode, 1984)/ *E. sp.* (Mossman Bluff, Henderson, 1997). Fossil stones of *E. clarkei* and *E. peterii* are similar in size, shape and inner mesocarp surface sculpture to fruit stones of extant *E. bancroftii* and *E. stellaris*, respectively, but differ in locule number. Rozefelds & Christophel (1996a, b) concluded that surface sculpture and shape of the fruit stone has potential for assessing affinities between fossil and extant taxa. Their 7 sculptural types provided the basis for delineating species groups among extant and fossil fruit stones of

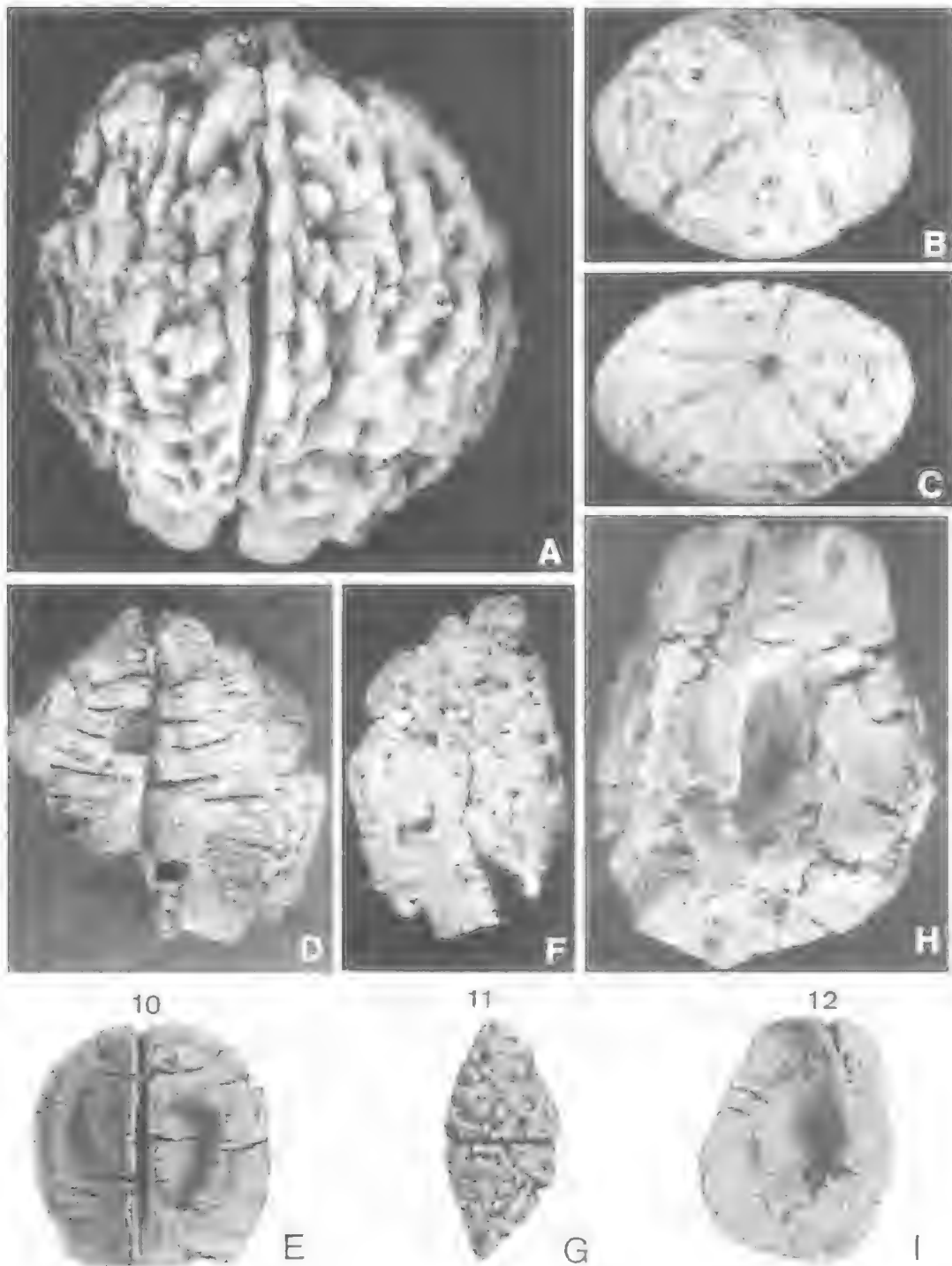


FIG. 21. *Elaeocarpus trachyclinis* (F.Muell.) Selling, fruit stones. Well preserved specimen consisting of two segments, $\times 2$; A, lateral view; B,C, apical and basal views of abraded specimen. D-G, lectotype comprising two segments that are abraded of original fruit stone, NMV53758. D, internal surfaces of two segments; E, external view of one segment; F, G, as illustrated in reverse by Mueller (1874a, pl. VIII, figs 10, 11), $\times \sim 1$. H, I, internal surface of fruit stone, $\times 2$; H, seed cavity; I, as illustrated in reverse by Mueller (1874a, pl. VIII, fig. 12), $\times \sim 1$.

TABLE 2. The fossil and extant Australian and New Zealand species of *Elaeocarpus* grouped into five stone-types on the basis of the sculptural attributes of their inner mesocarps as defined. To facilitate comparison the ornamentation types of Rozefelds & Christophel (1996b) are given in parentheses. Extant species as listed in Hnatiuk (1990). * Coode, 1984; Henderson, 1997.

Stone type	Sculptural attributes	Fossil taxa	Extant taxa
Type 1	Surface with raised sculpture; basal diameter of elements (usually high relief bacula, verrucae and/or rugulae); transverse diameter of fruit stone > 0.1 (baculate, bastionate, verrucate, echinate in part)	<i>E. cerebriformis</i> , <i>E. cunningii</i> , <i>E. johnstonii</i> , <i>E. mackayi</i> , <i>E. muelleri</i> , <i>E. spackmaniorum</i>	<i>E. angustifolius</i> , <i>E. arnhemicus</i> , <i>E. caroliniae</i> , <i>E. coorangooloo</i> , <i>E. culminicola</i> , <i>E. eumundi</i> , <i>E. holopetalus</i> , <i>E. kironit</i> , <i>E. obovatus</i> , <i>E. reticulatus</i> , <i>E. ruminatus</i> , <i>E. williamsianus</i> , <i>E. sp. nov.</i> 1*
Type 2	Surface with raised sculpture; basal diameter of elements (usually low relief verrucae, rugulae, grana); transverse diameter of fruit stone < 0.1 (echinate in part, granulate)	<i>E. lynchii</i> , <i>E. trachyclinis</i>	<i>E. costatus</i> , <i>E. dentatus</i> , <i>E. elliffii</i> , <i>E. hookerianus</i> , <i>E. grahamii</i> , <i>E. sericopetalus</i>
Type 3	Surface with pits or foveolae (punctate)	<i>E. allportii</i> , <i>E. brachyclinis</i> , <i>E. clarkei</i> , <i>E. peterii</i> , <i>E. rozefeldsii</i> (?)	<i>E. bancroftii</i> , <i>E. linsmithii</i> , <i>E. stellaris</i>
Type 4	Surface smooth or near smooth (smooth)	<i>E. angulare</i> , <i>E. bivalve</i> , <i>E. pleioclinis</i>	<i>E. ferruginiflorus</i> , <i>E. foveolatus</i> , <i>E. largiflorens</i> , <i>E. johnsonii</i> , <i>E. thelmae</i>
Type 5	Surface with fossulae	<i>E. couchmanii</i>	Not known

from Australia and New Zealand (Rozefelds & Christophel, 1996b); neither shape of the fruit stone nor locule number was utilized in their classification. Three of the categories – smooth, punctate and granulose – are well characterised, but mild abrasion of granulose fruit stones may reduce the sculpture to smooth and thus far fossil fruit stones having granulose sculpture remain unrecorded. Moreover, sculptural types distinguished as ‘verrucate’, ‘echinate’, ‘baculate’, and ‘bastionate’ (Rozefelds & Christophel, 1996b, table 2) may be difficult to uphold as exemplified by *E. angustifolius* whose fruit stone sculpture is said to be bastionate. The sculpture comprises a mix of bacula (straight-sided, flat crested elements), echinae (tapering, pointed processes), and distally expanded processes with flat, pointed or rounded crests, and these elements may be coalesced to form rugulae (Figs 5, 6). Furthermore, they described the fruit stones of *E. reticulatus* as echinate, but the elements include both round-topped (verrucae) and pointed (echinae) processes (Fig. 7).

Sculptural elements, particularly the distal crests of raised elements, may be substantially modified from their original form by abrasion during transportation. Even so, the bases of elements are likely to be preserved in all but extremely abraded fruit stones. The alternative grouping proposed here for stones with raised sculpture is based on the basal diameter of the sculptural elements relative to the transverse diameter of the fruit stone (Table 2). Many of the fossil taxa with raised sculpture included within Types 1 and 2 have sculptural patterns composed of a mix of bacula, verrucae, echinae and rugulae,

and each includes the baculate, bastionate, echinate and verrucate ornamentation classes of Rozefelds & Christophel (1996b, table 2). Types 3 and 4 accommodate taxa with punctate and smooth fruit stones respectively and Type 5 includes taxa with fossulate sculpture, a sculptural type not represented among extant Australian and New Zealand species (Table 2).

The fruit stone fossil record confirms that *Elaeocarpus* in eastern Australia dates to at least the Early Oligocene (Fig. 22) and corroborates evidence from cuticles and leaves (Carpenter, 1994). There are older (Eocene) records of leaves and cuticle of Elaeocarpaceae (*Elaeocarpus* or *Sloanea*) and of *Elaeocarpus*-like pollen from eastern Australia, but these await detailed systematic resolution (Truswell et al., 1987; Rowett, 1991; Rowett & Sparrow, 1994; Christophel, 1994). A Late Paleocene, leaf/cuticle record of the family is known from Cambalong Creek, Victoria (Valdala & Greenwood, in press). Thus far, reliable fossil records of fruits/leaves of Elaeocarpaceae indicate a geographic range from southernmost Tasmania north to central Queensland and west to southern South Australia. A range to northern South Australia may be implied by Late Paleocene–Early Eocene pollen (Martin, 1998). This distribution varies from its present range insofar as *Elaeocarpus* is no longer represented in South Australia or Tasmania. In New Zealand the Elaeocarpaceae has a history extending to at least the early Miocene as attested by leaves (Pole, 1993, 1996), but indubitable fossil fruits of *Elaeocarpus* are thus far unreported from pre-Quaternary sediments.















	QUEENSLAND	NEW SOUTH WALES	VICTORIA	TASMANIA	SOUTH AUSTRALIA	NEW ZEALAND
SERIES EPOCHS FRUIT TYPE	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5
Present-day						
Pleistocene						
Pliocene						
Miocene						?
Oligocene						
Eocene						
Paleocene						

FIG. 22. Recorded distribution and stratigraphic range of *Elaeocarpus* fruit stone types as defined in Table 2. Broken lines indicate age uncertainties of sediments; ? indicates uncertain record.

Not only has the genus distribution changed in Australia since the mid-Tertiary, so too have the distributions of species groups that shed the individual stone types (Table 2). Today species with Type 1 fruit stones are distributed from northernmost Tasmania to N Queensland, but during the mid-Tertiary ranged westward into S South Australia (Fig. 22). Type 2 fruit stones are shed by taxa that today occur in NSW (Lord Howe Island), Queensland and NZ in contrast to their more southerly and westerly mid-Tertiary distribution range of Victoria, NSW and South Australia. Extant species that have pitted fruit stones (Type 3) are restricted to N Queensland and NT, whereas during the mid-Tertiary this type had an E Australian distribution from S Tasmania to central Queensland. The mid-Tertiary distribution of smooth stones (Type 4) included Victoria and NSW, whereas today taxa with smooth stones are restricted to Queensland and regions to the north (Fig. 22). The record also implies a former higher species diversity in the region. Type 5 stones, without living counterpart in Australia, are present in Tertiary sediments of Victoria, NSW and South Australia (Fig. 22).

ACKNOWLEDGEMENTS

We are particularly grateful to Tim Spencer, South Blackwater Coal and Graham Muggerridge, Sandy Menpes and Howard

Rewald, CRA for charcoalfied fossils and locality details and to Gordon Guymer, Queensland Herbarium, for advice on the taxonomy of *Elaeocarpus*. Natalie Camilleri, Queensland Museum provided advice and assistance with photography and preparation of the diagrams. We acknowledge helpful discussions with, and comments from, Andrew Rozefelds who also kindly provided illustrations from his Honours thesis and a manuscript copy of Rozefelds & Christophel (in press). Advice on literature was also provided by Miguel Garcia, Sydney Botanical Garden, John Rigby, Queensland University of Technology, and Anthony Valdala, University of Melbourne. We thank Elizabeth Thompson, Museum of Victoria, Robert Jones, Australian Museum, and Ian Percival, Geological Survey of NSW for loan of material. Lin Sutherland and Julian Hollis, Australian Museum provided much helpful advice on basalt ages. MED thanks the Director, Queensland Museum for providing facilities and acknowledges support from The Australian Research Council during tenure of a Senior Research Fellowship.

LITERATURE CITED

- ALLEY, N.F. 1995. Barossa Basin. Pp. 173-175. In Drexel, J.F. & Preiss, W.V. (eds) The geology of South Australia, v.2 (Geological Survey of South Australia: Adelaide).

- BARNARD, C.E. 1881. Notes relating to certain fossil leaves and fruits found in the auriferous drifts of Gulgong, New South Wales. Papers and Proceedings and Report of Royal Society of Tasmania for 1880: 40-43.
- BERRY, E.W. 1926. *Cocos* and *Phymatocaryon* in the Pliocene of New Zealand. American Journal of Science 12: 181-184.
- BLACKBURN, D.T. & SLUITER, I.R. 1994. The Oligo-Miocene coal floras of southeastern Australia. Pp. 328-367. In Hill, R.S. (ed.) History of the Australian vegetation: Cretaceous to Recent (Cambridge University Press: Cambridge).
- BURROWS, C.J. 1997. An interglacial macrofossil flora from Schulz Creek, north Westland, New Zealand. New Zealand Journal of Botany 35: 187-194.
- CARPENTER, R.J., HILL, R.S. & JORDAN, G.J. 1994. Cenozoic vegetation in Tasmania: macrofossil evidence. Pp. 276-298. In Hill, R.S. (ed.) History of the Australian vegetation: Cretaceous to Recent (Cambridge University Press: Cambridge).
- CHRISTOPHEL, D.C. 1994. The early Tertiary macrofloras of continental Australia. In Hill, R.S. (ed.) History of the Australian vegetation: Cretaceous to Recent: 262-127. (Cambridge University Press: Cambridge).
- CLIFFORD, H.T. & DETTMANN, M.E. (in press). Drupe – a term in search of a definition. *Austrobaileya*.
- COODE, M.J.E. 1978. A conspectus of Elaeocarpaceae in Papuasias. *Brunonia* 1: 131-302.
1984. *Elaeocarpus* in Australia and New Zealand. *Kew Bulletin* 39: 509-586.
- CORNER, E.J.H. 1976. The seeds of the dicotyledons. (Cambridge University Press: Cambridge).
- DEANE, H. 1925. Tertiary fossil fruits from deep lead, Foster, south Gippsland. Records of the Geological Survey of Victoria 4: 489-492.
- DULHUNTY, J.A. 1971. Potassium-Argon dates and their significance in the Ilford-Mudgee-Gulgong region. *Journal and Proceedings of the Royal Society of New South Wales* 104: 39-44.
- ETTINGSHAUSEN, C. von. 1883. Beiträge zur Kenntniss der Tertiärflores Australiens. *Denkschriften Kaiserlichen Akademie Wissenschaften Wien* Part 1, 47:101-148.
1886. Beiträge zur Kenntniss der Tertiärflores Australiens. *Denkschriften Kaiserlichen Akademie Wissenschaften Wien* Part 2, 53: 81-184.
1888. Contributions to the Tertiary flora of Australia. *Memoirs of the Geological Survey New South Wales, Palaeontology* 2: 1-189, pls 1-15.
- FORSYTH, S.M. 1989. The Tamar Graben. Special Publication of the Geological Society of Australia 15: 358-361.
- GREENWOOD, D.R., VALDALA, A.J.V. & DOUGLAS, J.G. 2000. Victorian Paleogene and Neogene macrofloras: a conspectus. *Proceedings of the Royal Society of Victoria* 112: 65-92.
- GILBERT, L. 1986. The Royal Botanic Gardens, Sydney. (Oxford University Press: Melbourne).
- HARRIS, W.K. & OLLIVER, J.G. 1965. The age of the Tertiary sands at Rowland Flat, Barossa Valley. *Quarterly Geological Notes, Geological Survey of South Australia* 13: 1-2.
- HENDERSON, R.F.J. (ed.) 1997. Queensland plants: names and distribution. (Queensland Herbarium, Queensland Department of Environment: Brisbane).
- HNATIUK, R.J. 1990. Census of Australian Vascular Plants. Australian Flora and Fauna Series. Number 11, (Australian Government Publishing Service: Canberra).
- HOSSFELD, P.S. 1949. The significance of the occurrence of fossil fruits in the Barossa Senkungsfeld, South Australia. *Transactions of the Royal Society of South Australia* 72: 252-258.
- ISAAC, M.J., HERZER, R.H., BROOK, F.J. & HAYWARD, B.W. 1994. Cretaceous and Cenozoic sedimentary basins of Northland, New Zealand. *Institute of Geological and Nuclear Sciences Monograph* 8.
- JOHNSON, R.W. 1989. Intraplate volcanism in eastern Australia and New Zealand. (Cambridge University Press and Australian Academy of Science: Cambridge).
- JOHNSTON, R.M. 1880a. Note on the discovery of *Spondylostrobos smythii* Muell., and other fossil fruits in the deep lead drift at Brandy Creek Goldfield. *Report of the Royal Society of Tasmania for 1879*: 25-27.
- 1880b. Notes on the relations of the yellow limestone (travertin), of Geilston Bay, with other fluvial and lacustrine deposits in Tasmania and Australia. *Report of the Royal Society of Tasmania for 1879*: 81-90.
1882. Note showing that the estuary of the Derwent was occupied by a fresh-water lake during the Tertiary Period. *Report of the Royal Society of Tasmania for 1881*: 7-21.
- KERSHAW, A.P., MARTIN, H.A. & MCEWEN MASON, J.R. 1994. The Neogene: a period of transition. Pp. 299-327. In Hill, R.S. (ed.) History of the Australian vegetation: Cretaceous to Recent. (Cambridge University Press: Cambridge).
- KIRCHHEIMER, F. 1935. Paläobotanische Mitteilungen I & II. *Zentralblatt für Mineralogie, Geologie und Paläontologie* 5: 178-183.
- LEE, D.W. 1991. Ultrastructural basis and function of iridescent blue colour of fruits in *Elaeocarpus*. *Nature* 349: 260-261.
- LULY, J., SLUITER, I.R. & KERSHAW, A.P. 1980. Pollen studies of Tertiary brown coals: preliminary analyses of lithotypes within the Latrobe Valley, Victoria. *Monash Publications in Geography* 23: 1-77.
- MABBERLEY, D.J. 1987. The plant book. (Cambridge University Press: Cambridge).

- MARTIN, H.A. 1998. Late Cretaceous-Cainozoic palynology of the Poonarunna No.1 well, central Australia. *Transactions of the Royal Society of South Australia* 122: 89-138.
- MEAKIN, N.S. & MORGAN, E.J. 1999. Explanatory Notes Dubbo 1:250000 Geological Sheet (2nd edition). (Geological Survey of New South Wales: Sydney).
- McMINN, A. 1981. A Miocene microflora from the Home Rule kaolin deposit. *Quarterly Notes, Geological Survey of New South Wales* 43: 1-4.
- MUELLER, F. von. 1871a. New vegetable fossils of Victoria. Reports of the Mining Surveyors and Registrars, Victoria. Quarter ending 30th June 1871: 47-49.
- 1871b. New vegetable fossils of Victoria. Reports of the Mining Surveyors and Registrars, Victoria. Quarter ending 30th September 1871: 39-41.
1873. New vegetable fossils of Victoria. Reports of the Mining Surveyors and Registrars, Victoria. Quarter ending 30th September 1873: 41-44.
- 1874a. New vegetable fossils of Victoria. Reports of the Mining Surveyors and Registrars, Victoria. Quarter ending 31st December 1873: 41-44.
- 1874b. New vegetable fossils of Victoria. Reports of the Mining Surveyors and Registrars, Victoria. Quarter ending 30th September 1874: 41-44.
- 1874c. Observations on new vegetable fossils of the auriferous drifts, Geological Survey of Victoria. (John Ferres, Government Printer: Melbourne).
1875. New vegetable fossils of Victoria. Reports of the Mining Surveyors and Registrars, Victoria. Quarter ending 30th June 1875: 41-43.
1876. Description of fossil plants from the Upper Tertiary auriferous drifts of New South Wales. *Annual Report of the Department of Mines, New South Wales for 1875*: 124-126.
1877. Descriptive notes on the Tertiary flora of New South Wales. *Annual Report of the Department of Mines, New South Wales for 1876*: 178-180.
1878. New vegetable fossils of Victoria. Reports of the Mining Surveyors and Registrars, Victoria. Quarter ending 30th September 1878: 38-40.
1879. Descriptive notes on the Tertiary flora of New South Wales. *Annual Report of the Department of Mines, New South Wales for 1878*: 169-172.
1882. New vegetable fossils of Victoria. Reports of the Mining Surveyors and Registrars, Victoria. Quarter ending 31st March 1882: 43-44.
1883. Observations on new vegetable fossils of the auriferous drifts. Second Decade, Geological Survey of Victoria. (John Ferres, Government Printer: Melbourne).
1885. References to Baron Constantin von Ettingshausen's recent observations on the Tertiary flora of Australia. *Papers and Proceedings of the Royal Society of Tasmania for 1884*: 203-207.
- MUELLER, F. von & SMYTH, R.B. 1870. Observations on some vegetable fossils from Victoria. *Geological Magazine*: 390.
- PARTRIDGE, A. 1993. Palynological analysis of four samples from deep leads near Stawell, Victoria. *Biostrata report 1993/21* (unpubl.).
1995. Palynology of intercalated sediments between flows of the Newer Volcanics in the Ballarat district. *Biostrata report 1995/11* (unpubl.).
- PARTRIDGE, A. & WILKINSON, H.E. 1982. Palynological examination of samples from the Woodstock 10008 bore, Loddon deep lead. *Geological Survey of Victoria Report 1982/11* (unpubl.).
- PICKETT, J.W., SMITH, N., BISHOP, P.M., HILL, R.S., MACPHAIL, M.K. & HOLMES, W.B.K. 1990. A stratigraphic evaluation of Ettingshausen's New England Tertiary plant localities. *Australian Journal of Earth Sciences* 37: 293-303.
- POLE, M. 1993. Early Miocene flora of the Manuhierikia Group, New Zealand. 5. Smilacaceae, Polygonaceae, Elaeocarpaceae. *Journal of the Royal Society of New Zealand* 23: 289-302.
1996. Plant macrofossils from the Foulden Hills Diatomite (Miocene), central Otago, New Zealand. *Journal of the Royal Society of New Zealand* 26: 1-39.
- REYNOLDS, S.J. 1985. Sapindaceae. In George, A.S. (ed.) *Flora of Australia*, v.25. Melianthaceae to Simaroubaceae. (Australian Government Publishing Service: Canberra).
- ROWETT, A.I. 1991. The dispersed cuticular floras of South Australian Tertiary coalfields, Part 1: Sedan. *Transactions of the Royal Society of South Australia* 115: 21-36.
- ROWETT, A.I. & SPARROW, A.D. 1994. Multivariate analysis of Australian Eocene dispersed cuticle floras: influence of age, geography and taphonomy on biozonation. *Review of Palaeobotany and Palynology* 81: 165-184.
- ROZEFELDS, A.C. 1990. A mid Tertiary rainforest flora from Capella, Central Queensland. Pp. 123-136. In Douglas, J.G. & Christophel, D.C. (eds) *Proceedings of the Third International Organization on Palaeobotany Symposium 1988*. (A-Z Printers: Melbourne).
- ROZEFELDS, A.C. & CHRISTOPHEL, D.C. 1996a. *Elaeocarpus* (Elaeocarpaceae) fruits from the Oligo-Miocene of eastern Australia. *Papers and Proceedings of the Royal Society of Tasmania* 130: 41-48.
- 1996b. *Elaeocarpus* (Elaeocarpaceae) fruits from the Early to Middle Miocene of eastern Australia. *Muelleria* 9: 229-237.
- In press. *Elaeocarpus* (Elaeocarpaceae) fruits from the Australian Cenozoic. *Alcheringa*.
- SELLING, O.H. 1950. Some Tertiary plants from Australia. *Svensk Botanisk Tidskrift* 44: 551-561.
- SUTHERLAND, F.L. 1995. The volcanic earth. (University of New South Wales Press: Sydney).
- SUTHERLAND, F.L., STUBBS, D. & GREEN, D.C. 1977. K-Ar ages of Cainozoic volcanic suites, Bowen-St. Lawrence hinterland, north

- Queensland (with some implications for petrologic models). *Journal of the Geological Society of Australia* 24: 447-460.
- TEDFORD, R.H., BANKS, M.R., KEMP, N.R. & SUTHERLAND, F.L. 1975. Recognition of the oldest known fossil marsupial from Australia. *Nature* 225: 141-142.
- THOMPSON, B.N. 1978. Tertiary Stratigraphy. Pp. 443-449. In Suggate, R.P., Stevens, G.R., Te Punga, M.T. (eds) *The geology of New Zealand* (Government Printer: Wellington).
- TRUSWELL, E.M., KERSHAW, A.P. & SLUITER, I.R. 1987. The Australian-south-east Asian connection: evidence from the palaeobotanical record. Pp. 32-49. In Whitmore, T.C. (ed.) *Biogeographical evolution of the Malay archipelago*. (Clarendon Press: Oxford).
- VALDALA, A.J.V. & GREENWOOD, D.R. (in press). Australian Paleogene vegetation and environments: evidence for palaeo-Gondwanan elements in the fossil records of Lauraceae and Proteaceae. In Metcalfe, I., Smith, J.M.B., Morwood, M. and Davidson, I. (eds) *Faunal and floral migrations and evolution in SE Asia-Australasia*. (A.A. Balkema: Rotterdam).
- WELLMAN, P. & McDOUGALL, I. 1974. Cainozoic igneous activity in eastern Australia. *Tectonophysics* 23: 49-65.

APPENDIX 1: Register of figured specimens. * denotes nomenclatural type.

Taxon	Fig. No.	Original Figure	Specimen Status	Locality	Repository/ Reg. No.
<i>E. angularis</i>	8A-F	Mueller, 18740c, pl. X, figs 1-4	Holotype *	Haddon (Smythe's Ck), Vic	NMVP53565,6017
<i>E. bivalve</i>	9A-C		Neotype *	Black lead, Gulgong, NSW	MMF36220
	9D-G		-	Forest reefs, Gulgong, NSW	AMF6669
	9I-LI		-	Black lead, Gulgong, NSW	MMF36221
	9J-K		-	Forest reefs, Gulgong, NSW	AMF6669
<i>E. brachyclinis</i>	10A-C	Mueller, 1874a, pl. VIII, fig. 4	Lectotype *	Haddon (Smythe's Ck), Vic	NMVP6060
	10E-G,I		-	Haddon, Vic	NMVP212639
	10H		-	Haddon, Vic	NMVP6025
	10J-L		-	Haddon, Vic	NMVP53918
<i>E. clarkei</i>	11A,B	Rozefelds & Christophel, 1996a, pl. 1, figs A-C	Neotype *	Elsmore, NSW	AMF9281
	11C-I		-	Victory Mine, Orange, NSW	AMF8440
<i>E. couchmanii</i>	12A-C	Mueller, 1882, pl. XIX, figs 3,11	Lectotype *	Haddon (Nintingbool), Vic	NMVP53920
	12F-G		-	Haddon, Vic	NMVP53921
<i>E. cunningii</i>	13A-D	Rozefelds, 1990, fig. 6D	Holotype *	Glencoe, Capella, Qld	QMF16768
	13E,F,G		-	Picardy Station, Morandah, Qld	QMF50114
	13H	Rozefelds 1990, fig. 6E	Paratype	Glencoe, Capella, Qld	QMF50115
	13I,J		-	Glencoe, Capella, Qld	QMF50116
	13K		-	Glencoe, Capella, Qld	QMF50117
	13L		-	Glencoe, Capella, Qld	QMF50118
<i>E. lynchii</i>	14A-C	Mueller 1871b, pl. IV, figs 1-4	Lectotype * (2 segments)	Haddon (Nintingbool), Vic	NMVP6034
			Lectotype * (1 segment)	Haddon (Nintingbool) Vic	NMVP6035
	14I-K		-	Haddon, Vic	NMVP53969
	14L-O		-	Smythesdale, Vic	QMF56119
<i>E. mackayii</i>	15A,B,I	Mueller, 1871a, pl. II, fig. 4; Rozefelds & Christophel, in press, fig. 2A,B	Lectotype *	Haddon (Smythe's Creek), Vic	NMVP53562
	15C		-	South Blackwater, Qld	QMF50120
	15D		-	Picardy Station, Morandah, Qld	QMF50121
	15E-G		-	Picardy Station, Morandah, Qld	QMF50122
	15H		-	Picardy Station, Morandah, Qld	QMF51078
<i>E. peteri</i>	16A-D	Rozefelds & Christophel, 1996b, pl. 3, figs A,C,E,G,I	Holotype *	Glencoe, Capella, Qld	QMF18088
<i>E. pleiochneis</i>	17A-C	Mueller, 1873, pl. VI, figs 3,4	Lectotype *	Haddon (Nintingbool), Vic	NMVP53747
	17F-G		-	Haddon, Vic	NMVP53741
	17H,I		-	Haddon, Vic	NMVP53741
	17J-M		-	Haddon, Vic	NMVP53741
<i>E. rozefeldsii</i>	18A,C	Mueller, 1873, pl. VI, figs 3,4	Holotype *	South Blackwater, Qld	QMF50123
	18B		-	South Blackwater, Qld	QMF50124
	18D		-	South Blackwater, Qld	QMF50125
	18E,F		-	South Blackwater, Qld	QMF50126
<i>E. spackmanianum</i>	19A-C	Rozefelds, 1990, figs 4A,B	Holotype *	Glencoe, Capella, Qld	QMF15440
	19D-I,J	Rozefelds, 1990, figs 4E,F	Paratype	Glencoe, Capella, Qld	QMF15442
	19G-I	Rozefelds, 1990, fig. 4G	Paratype	Glencoe, Capella, Qld	QMF15444
	19K-M		-	Glencoe, Capella, Qld	QMF50127
	20A-D		-	Picardy Station, Morandah, Qld	QMF51076
	20E,F		-	Picardy Station, Morandah, Qld	QMF51077
<i>E. trachyclinis</i>	21A		-	Haddon, Vic	NMVP53984
	21B,C		-	Haddon (Smythe's Creek) Vic	NMVP53922
	21D,F	Mueller, 1874a, pl. VIII, figs 10,11	Lectotype *	Haddon, Vic	NMVP53758



DUSK CHORUSING BEHAVIOUR IN CICADAS (HOMOPTERA: CICADIDAE) AND A MOLE CRICKET, BRISBANE, QUEENSLAND

TONY EWART

Ewart, A. 2001 06 30: Dusk chorusing behaviour in cicadas (Homoptera: Cicadidae) and a mole cricket, Brisbane, Queensland. *Memoirs of the Queensland Museum* 46(2): 499-510. Brisbane. ISSN 0079-8835.

Diurnal singing behaviour is documented for 9 SE Queensland cicadas, from *Arianta*, *Psaltoda* and *Pantropsalta*, with particular reference to the presence/absence of dawn/dusk chorusing. This occurs more within relatively sedentary and also aggregating species. Detailed documentation of dusk chorusing during November 1996-April 1997 in inner city St Lucia, Brisbane, is presented for 5 cicadas *Cystosoma saundersii* Westwood, *Glauco-psaltria viridis* Goding & Froggatt, *Tamasa tristigma* (Germar), *Abrieta curvicauda* (Germar), and *Psaltoda charlpenis* Ashton, and the mole cricket (*Gryllotalpa pluvialis* Mjöberg). The choruses closely follow, seasonally, the sunset and civil twilight curves, except for *T. tristigma* which systematically changes its pattern during the season. Extensive interspecific synchrony of chorusing occurs at the same location, although chorus start/finish times vary between species. Factors controlling chorusing behaviour, especially light intensity and ambient temperature, and the importance of the distinctive interspecific song characteristics, are discussed. □ *Cicadas, mole cricket, chorusing behaviour: Brisbane.*

A. Ewart, Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; 13 October 2000

Many southeastern Queensland (SEQ) cicadas exhibit both extended daytime singing plus short and intense bursts of dawn and/or dusk chorusing. Certain species are crepuscular, with singing restricted to dusk, the best known local example being the Bladder Cicada, *Cystosoma saundersii* Westwood. Not all cicadas, however, exhibit dawn/dusk chorusing and observations over 30 years suggest that the behaviour is best developed in: 1) relatively localised and sedentary cicada species, and 2) aggregating species, many of which are also localised.

Comparable dawn/dusk chorusing behaviour is documented worldwide, including Malaysia (Gogola & Riede, 1995); New Mexico (Crawford & Dadone, 1979); Tennessee (Sanborn, 2000); Mexico (Moore, 1962); Borneo (Riede, 1996, 1997; Reide & Kroker, 1995); Costa Rica (Young 1976; 1982:102); Thailand (Gogola, 1995); Fiji (Duffels, 1988); Southern Africa (pers. obs.). Myers (1929: 206-7, 221) quoted further examples from South America, New Zealand, the Philippines and the Himalaya.

The main feature of these choruses are their short, but predictable (day to day) timing and duration, and their intensity. Only severe late afternoon storms seem to modify their timing. In SEQ, strongly mobile cicada species rarely produce defined dawn/dusk choruses, but instead

sing more or less continuously throughout the day from early morning to near dusk.

This report outlines observed cicada singing behaviour in a variety of species in SEQ and, in particular, more detailed documentation, over 6 months, of dusk chorusing of 5 cicada and 1 Orthopteran species from suburban St Lucia, central Brisbane (27°29.63'S, 153°00.04'E). All 6 species could be heard singing synchronously within the same localised area. This account starts by reporting more general observations of diurnal singing patterns in SEQ.

DIURNAL CICADA SONG PATTERNS

Two widespread but relatively sedentary mangrove-inhabiting cicadas, *Arianta interclusa* (Walker) and *Psaltoda plaga* (Walker), provide examples of both strong day and dawn/dusk chorusing (Fig. 1). Both species are medium to larger sized cicadas (♂ body lengths [MBL] 27-33 and 27-39mm, respectively) with relatively sedentary behaviour patterns. Both exhibit strong diurnal singing, starting between 0600-0700 hours (Eastern Standard Time), with progressive reduction in intensity during mid to late afternoon until cessation at approximately 1700 hours. Dusk chorusing occurs immediately following sunset, being less intense for *P. plaga*. Dawn chorusing commences immediately prior to sunrise. Although dawn chorusing is more poorly developed in *P. plaga*, it commences its

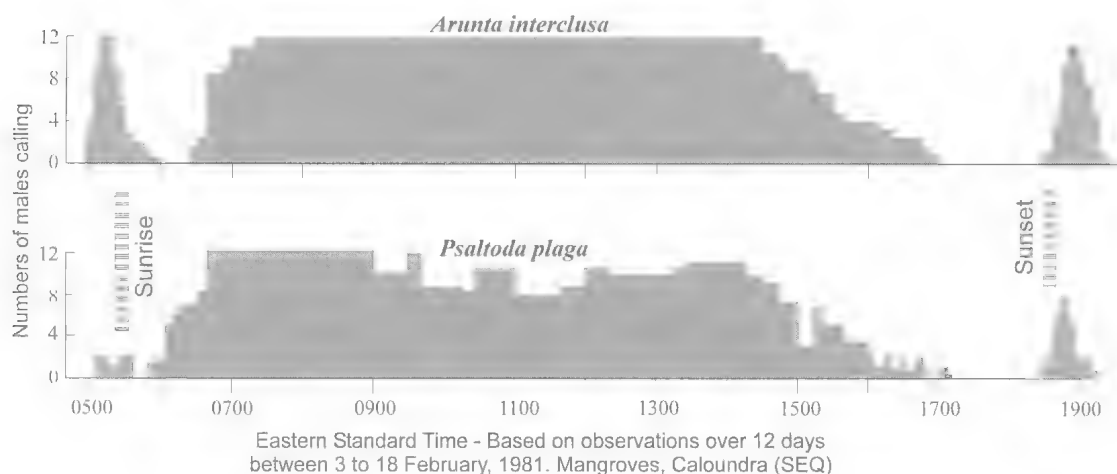


FIG. 1. Daytime singing patterns of two mangrove dwelling cicadas. The graphs are compiled from regular daily observations, at intervals of 15-20 minutes, of times at which songs of each species are heard within a given habitat. The sunrise/sunset times are shown for the period of observation.

diurnal singing slightly earlier than *A. interclusa*. *P. plaga* normally forms relatively dense singing aggregations with short but frequent flights, this behaviour being less pronounced in *A. interclusa*. Both species sing from inner and outer mangrove branches which allows micro-habitat selection for variable shade conditions. Mangroves, in fact, are subjected to direct and also indirect solar radiation from reflection off surrounding water and wet mud surfaces. The afternoon decrease in

song activity is presumably a behavioural response by the insects to avoid superheating (i.e. exceeding thermal tolerances; Sanborn, 1997).

Psaltoda claripennis Ashton, *Psaltoda harrisii* (Leach) and *Tamasa tristigma* (Germar) (Fig. 2) illustrate further examples of song patterns. Both *Psaltoda* species are medium to larger sized cicadas (MBL 24-34 and 22-29mm, respectively) and widespread throughout SEQ. *P. claripennis* forms localised singing aggregations in suburban

and open forest habitats while *P. harrisii* is restricted to open forest and wallum communities, again normally in localised aggregations. *P. claripennis* produces a strong dusk chorus, but no dawn chorus, whereas *P. harrisii* surprisingly exhibited neither during the observation period. Both are strong diurnal singers, with *P. claripennis* showing a marked reduction of song intensity during the midday period. As both species sing from exposed tree branches, reduction and later afternoon cessation of song seems to represent behavioural thermoregulation and allow feeding (Sanborn, 1997). *T. tristigma* is a very

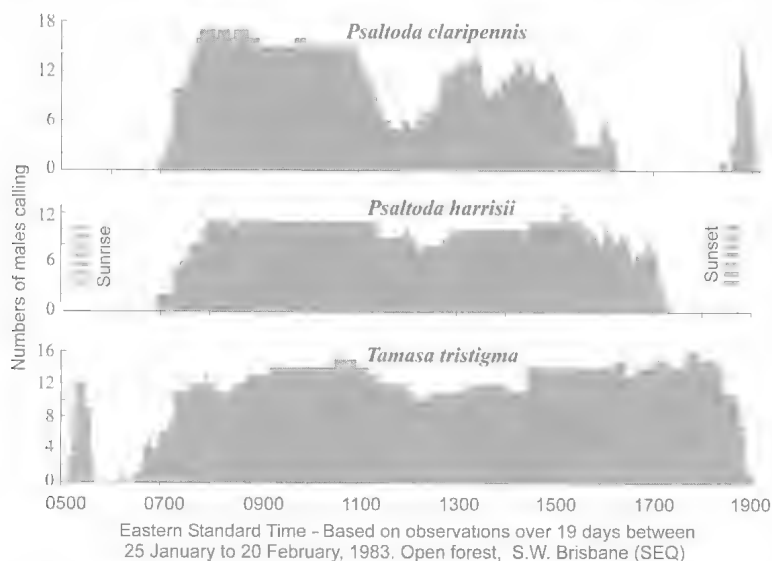


FIG. 2. Daytime singing patterns of three open woodland/suburban cicadas. Data compiled as in Fig. 1.

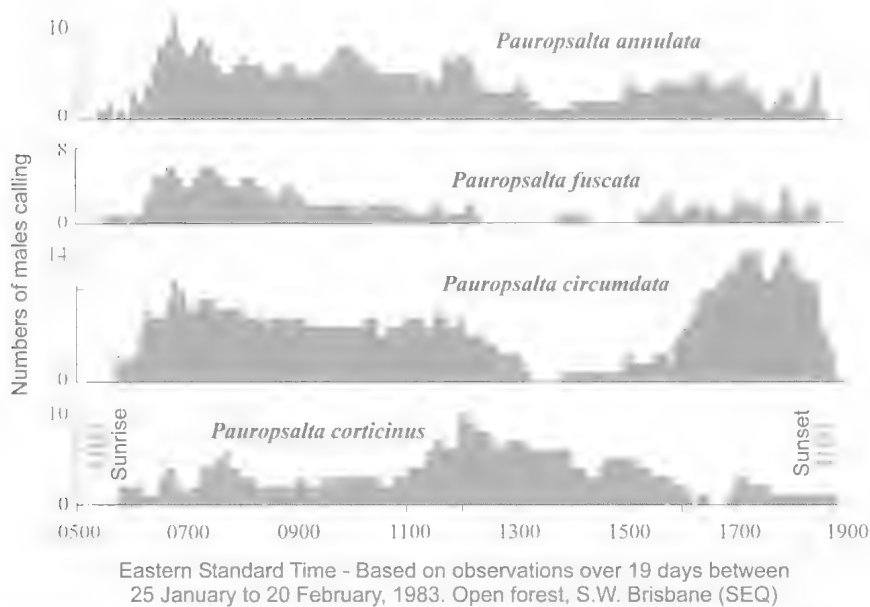


FIG. 3. Daytime singing patterns of four open woodland *Pauropsalta* cicadas. Data compiled as in Fig. 1.

common, medium sized (MBL 16-23mm), rather sedentary species of open forest and suburban areas. Singing occurs from exposed tree trunks. It exhibits a strong dawn chorus (coinciding with sunrise), followed at about 0700 by the beginning of the extended diurnal song period. This cicada is also notable for the fact that it regularly sings strongly during rain. As shown below, the late afternoon to dusk singing behaviour changes from early summer through to autumn, with discrete dusk chorusing only occurring early and late in a given summer season.

Singing patterns of 4 *Pauropsalta* species (Fig. 3) show further variations. *P. fuscata* Ewart, *P. corticinus* Ewart and *P. annulata* Goding and Froggatt (MBL 12-17, 14-18 and 11-15mm, respectively) are small, cryptic and highly mobile species, common in open forests and wallum habitats (Ewart, 1989). *P. annulata* is a foliage dweller, while *P. fuscata* and *P. corticinus* provide good examples of 'sing and fly' behaviour (e.g. Sanborn, 1997; Duffels, 1988: 74). Singing occurs from open tree trunks and branches, posts, etc., where their dominantly black coloration facilitates thermoregulation from solar radiation, with additional endogenous heat provided from frequent flight activity (e.g. Sanborn, 1997, 2000). Singing occurs throughout the day, extending to late afternoon, but they do not exhibit discrete dawn/dusk chorusing. This is believed to result from their smaller body size which precludes significant heat retention once

solar radiation ceases to be effective (M. Coombs, pers. comm.).

Pauropsalta circumdata (Walker) is a slightly larger (MBL 18-21mm) member of the genus, relatively sedentary, singing from open branches of medium to tall eucalypts, usually well exposed to solar radiation. No discrete dawn/dusk chorus is emitted. Diurnal song production extends through the morning, with a clear period of suspended activity during early-mid afternoon, followed by intense singing from late afternoon extending to dusk. This final phase incorporates the 'dusk chorus' time interval. During this late afternoon/dusk phase, the insects remain exposed to the sun allowing them to sing until solar radiation effectively ceases.

EVENING CHORUS SYNCHRONY IN FIVE CICADA AND ONE MOLE CRICKET SPECIES

Start and finish times for the dusk choruses of *Glaucopsaltria viridis* Goding & Froggatt (Bottle Cicada), *C. saundersii* (Bladder Cicada), *Abrieta curvica* (Germar) (plus *P. claripennis*), *T. tristigma*, and the mole cricket *Gryllotalpa pluvialis* Mjöberg, are illustrated for a 6 month period (Figs 4-6). Each species sang within a localised suburban habitat, the songs each being easily heard from the single observation location. The choruses are compared with sunset and civil twilight times (data from Astronomical Applications Dept., U.S. Naval

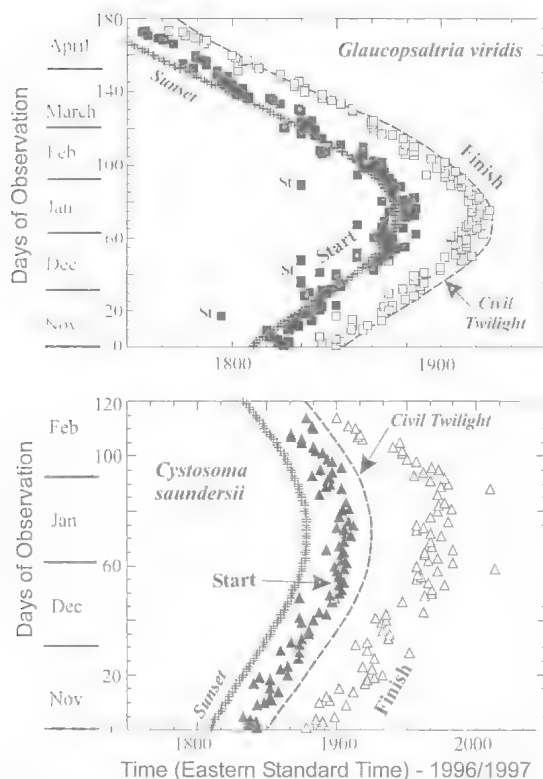


FIG. 4. Dusk singing patterns, over 4-6 month intervals, of *G. viridis* and *C. saundersii*, from St Lucia, Brisbane City. The solid symbols indicate start, and hollow symbols finish, of dusk choruses. 'St' against a symbol indicates storm. Sunset and civil twilight curves are plotted for comparison.

Observatory, Washington). The plots highlight the close correspondence between the seasonally changing dusk chorus timing and light intensity. Sunset is formally defined as the moment the uppermost point of the sun appears to vanish below the horizon and civil twilight as the time between sunset and the moment the sun reaches a point lying 6° below the horizon (Beck, 1980; Nielsen, 1963).

Although a similar result could no doubt be obtained with sky light intensity measurements (e.g. Crawford & Dadone, 1979), such measurements do not allow for the differing micro-habitat niches of the cicadas. *C. saundersii* and *G. viridis* are both cryptic, green, crepuscular species which inhabit dense foliage, whose main song periods are at dusk (see also Doolan & MacNally, 1981; *G. viridis* does produce brief singing and clicking during the day, especially when overcast). *C. saundersii* and *G. viridis* are large to medium sized cicadas (MBL 39-53 and

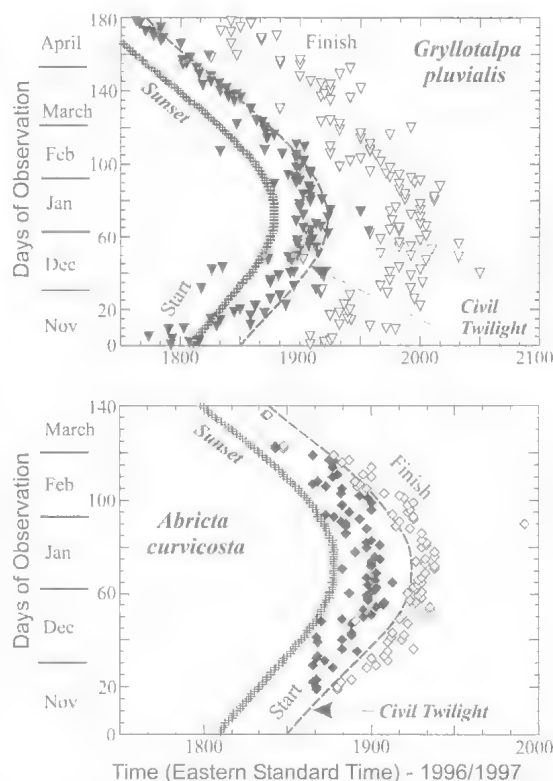


FIG. 5. Dusk singing patterns, over 5-6 month intervals, of *A. curvica* and the Common Mole Cricket, *G. pluvialis*. Filled and hollow symbols indicate start/finish of dusk chorusing. Sunset/civil twilight curves are shown for comparison.

26-35mm, respectively) with abnormally enlarged abdomens, and consequently relatively poor flight. *A. curvica* (MBL 25-31mm) occurs on tree trunks, normally partly hidden by foliage, while *P. claripennis* and *T. tristigma* sing from more open tree trunks and branches. The mole cricket occurs in shallow soil burrows. Absolute light intensities will vary within these different microhabitats at any given time. Nevertheless, the mole cricket data are less regular than the corresponding cicada data, possibly due to variable diurnal and seasonal shadow effects over their fixed burrow positions. Rain flooding of their burrows presumably explains 'non-singing' during and following afternoon storms. The dusk chorusing of *P. claripennis* overlapped extensively with, and was largely masked by the singing of *A. curvica*. Although the 2 species commenced dusk chorusing nearly simultaneously, *P. claripennis* stopped earlier.

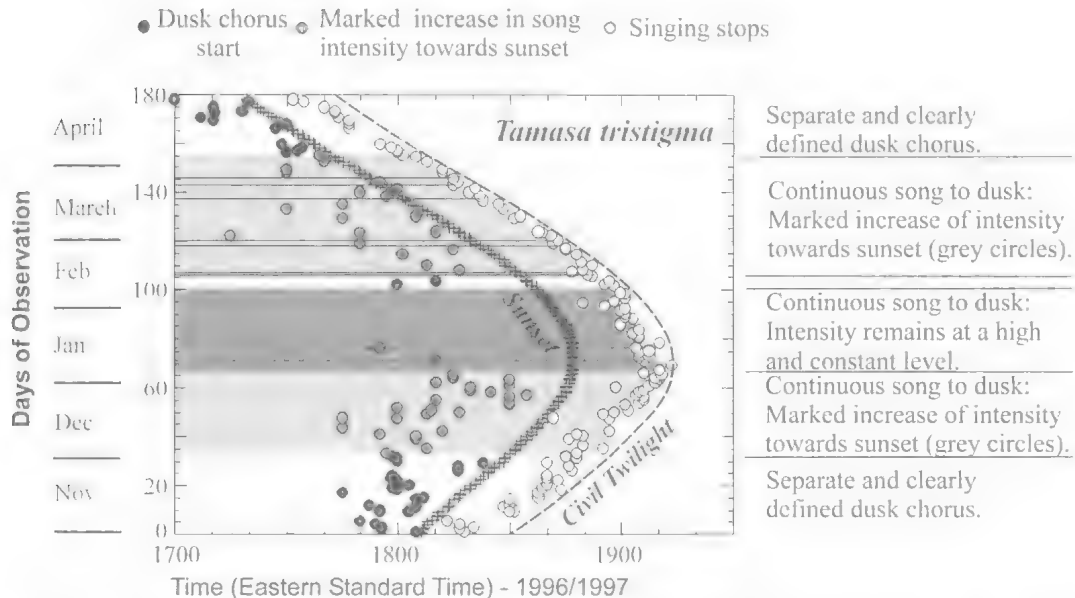


FIG. 6. Dusk singing patterns, over 6 month interval, of *T. tristigma* showing the seasonal changes of afternoon/dusk singing behaviour, noting that singing cessation is consistent throughout. The solid and dotted lines represent isolated days of anomalous singing behaviour relative to each behavioural segment. True dusk chorusing is restricted to early and late in season. Sunset/civil twilight curves are shown for comparison. See also Fig. 8D.

T. tristigma shows a systematic change of singing patterns from early summer through to autumn (Fig. 6). Discrete dusk chorusing occurs in early and late summer season (November and April), with a very brief additional occurrence in early February. In mid-summer (mostly January), singing is continuous at relatively high intensities through until near civil twilight. The periods either side of mid-summer (December and February/March) have continuous singing through to civil twilight, but with marked increases in intensity in late afternoon/dusk (i.e. intermediate behaviour to discrete dusk chorusing). At all times during summer, however, singing consistently ends close to the civil twilight curve, irrespective of whether a discrete dusk chorus, or continuous late afternoon to dusk singing occur.

Although clearly correlated with fading light, triggering mechanisms of dusk chorusing may be more complex. These include (Crawford & Dadone, 1979; Riede & Kroker, 1995): i) total light intensity; ii) rate of change of light intensity; iii) changing spectral composition of evening light, such as the suppression of middle wavelengths of visible light (Endler, 1992); and iv) barometric pressure changes prior to dusk.

Some support for a more complex triggering mechanism, for start of dusk chorus, is provided by the lack of statistically significant differences between fine to cloudy/overcast days (Table 1), although the means do show systematic shifts. Only severe late afternoon storms caused the early onset of dusk chorusing (points labeled 'st' in Fig. 4). Another relevant aspect is the small seasonal variation of twilight period (i.e. between sunset and civil twilight), 0.40–0.47 hour for the total observation period.

The close correlations between start and finish of dusk choruses and sunset/civil twilight curves, for each species, are illustrated further by Pearson correlation coefficients (r) derived from the linear plots between these variables (e.g. Fig. 7D). The coefficients between sunset and chorus start (finish) times or *G. viridis*, *C. saundersii*, *T. tristigma*, *A. curvicauda* and *G. pluvialis* are, respectively, 0.96 (0.99, $n=121$); 0.95 (0.88, $n=84$); (0.99, finish only, $n=121$); 0.85 (0.88, $n=76$); and 0.89 (0.86, $n=117$). Identical values are calculated using civil twilight instead of sunset times. The correlation coefficients are high, especially those for *T. tristigma* (chorus finish), *G. viridis*, and chorus onset of *C. saundersii*, pointing to absolute light intensity as

TABLE 1. Dusk chorus starting times, relative to sunset, under clear and cloudy conditions, chorus duration's, reference CREP data, ambient temperatures (T_a) and temperature gradients during dusk chorusing. Data presented as means and standard deviations (in parentheses). * Chorus finish only.

	<i>T. tristigma</i>	<i>G. viridis</i>	<i>C. saundersii</i>	<i>A. curvicauda</i>	<i>G. pluvialis</i>
(Chorus start – sunset) (hrs). All data	0.32 (0.07)*	0.030 (0.11)	0.26 (0.06)	0.24 (0.09)	0.29 (0.21)
(Chorus start – sunset) (hrs). Clear to <50% cloud cover	-	0.075 (0.071) (n = 77)	0.28 (0.052) (n = 46)	0.26 (0.086) (n = 39)	0.33 (0.16) (n = 74)
(Chorus start – sunset) (hrs). Overcast to >50% cloud cover	-	-0.031 (0.12) (n = 44)	0.23 (0.068) (n = 38)	0.22 (0.086) (n = 37)	0.23 (0.26) (n = 43)
Chorus duration (hrs). All data	-	0.33 (0.09)	0.61 (0.16)	0.29 (0.14)	0.87 (0.34)
CREP; chorus start. All data	-	0.087 (0.25)	0.59 (0.15)	0.54 (0.20)	0.68 (0.49)
CREP; chorus finish. All data	0.74 (0.16)	0.86 (0.13)	1.97 (0.35)	1.19 (0.27)	2.69 (0.56)
T_a at chorus start ($^{\circ}\text{C}$). All data	24.2 (1.9)	23.8 (1.7)	23.6 (1.8)	24.0 (1.5)	23.5 (1.7)
T_a at chorus finish. ($^{\circ}\text{C}$). All data	23.5 (1.7)	23.5 (1.7)	23.3 (1.8)	23.8 (1.5)	23.0 (1.8)
Temperature gradient during dusk chorus ($^{\circ}\text{C}$). All data	0.8 (0.8)	0.3 (0.4)	0.3 (0.6)	0.2 (0.3)	0.9 (0.8)
Total T_a range during dusk chorus ($^{\circ}\text{C}$)	18-30	19-29	18-29	21-27	18-29
n (number of data)	121	121	84	76	117

the dominant control on the timing of dusk chorusing. The coefficients for *C. saundersii* (finish), *G. pluvialis* and to a less extent *A. curvicauda*, are numerically lower, reflecting the fact that chorusing ceases well after twilight, indicating additional controlling factor(s). Even for *G. viridis*, there is a discernible deviation of the chorus starting time, relative to sunset, early and late during the summer season (Fig. 7D). This also suggests secondary controlling factors, possibly seasonally changing spectral properties of the evening light. An alternative time parameter that has been advocated for such studies is the crepuscular time unit (CREP; Nielsen, 1963; Beck, 1980). Although noted in Table 1, this parameter was not found to be as useful in this study as simpler comparative plots using standard sunset and twilight data.

The possible influence of ambient temperature (T_a) and temperature gradients on chorusing patterns are evaluated from temperature data, taken every 30 minutes during the whole period of observation, from records for Brisbane from the Australian Bureau of Meteorology. These data were linearly extrapolated to the seasonal starting and finishing times of chorusing for each species. T_a ranged between 18-30 $^{\circ}$ during chorusing, averaging between 23-24 $^{\circ}$ (Tables 1 and 2) during the 6 month observation period. These temperature ranges suggest that T_a is not a controlling factor in triggering or controlling the duration of dusk (or dawn) chorusing. This is confirmed, for all 5 species, by the lack of

significant correlation's between the start and finish of dusk choruses and T_a (r values range between -0.22 and 0.42) or between temperature gradients during chorusing and the start/finish timing of the choruses (r values -0.24 to 0.35). It is recognised, however, that for singing to occur, body temperature needs to exceed some critical minimum value for each species (Sanborn, 1997, 2000), although this is in part controlled by T_a . Josephson & Young (1979) indicated that *C. saundersii* ♂♂ are ectothermic. It is unknown whether this also applies to the other cicadas considered here. Nevertheless, the patterns of singing behaviour and habitats of *G. viridis* and *T. tristigma* males suggest possible ectothermy.

Chorus duration (Fig. 7A; Table 2) for *C. saundersii* increases during the summer season, but sharply decreases at the end of its season, believed to reflect a combination of slightly shorter twilight period and especially the diminishing and aging population. *G. viridis*, and *A. curvicauda* exhibit shorter chorus lengths both early and late in the season (Fig. 7B,C; Table 2), thought to also reflect smaller population and twilight length effects. *G. pluvialis* shows no systematic seasonal change of chorus length. Reference to the seasonal variation of T_a 's for dusk chorus finish (\approx start) times for *G. viridis* (Fig. 8A) suggest that seasonal T_a variations could have a significant effect in determining seasonal changes in chorus duration. This is negated, however, by: i) the lack of significant correlation's, for all five species, between chorus

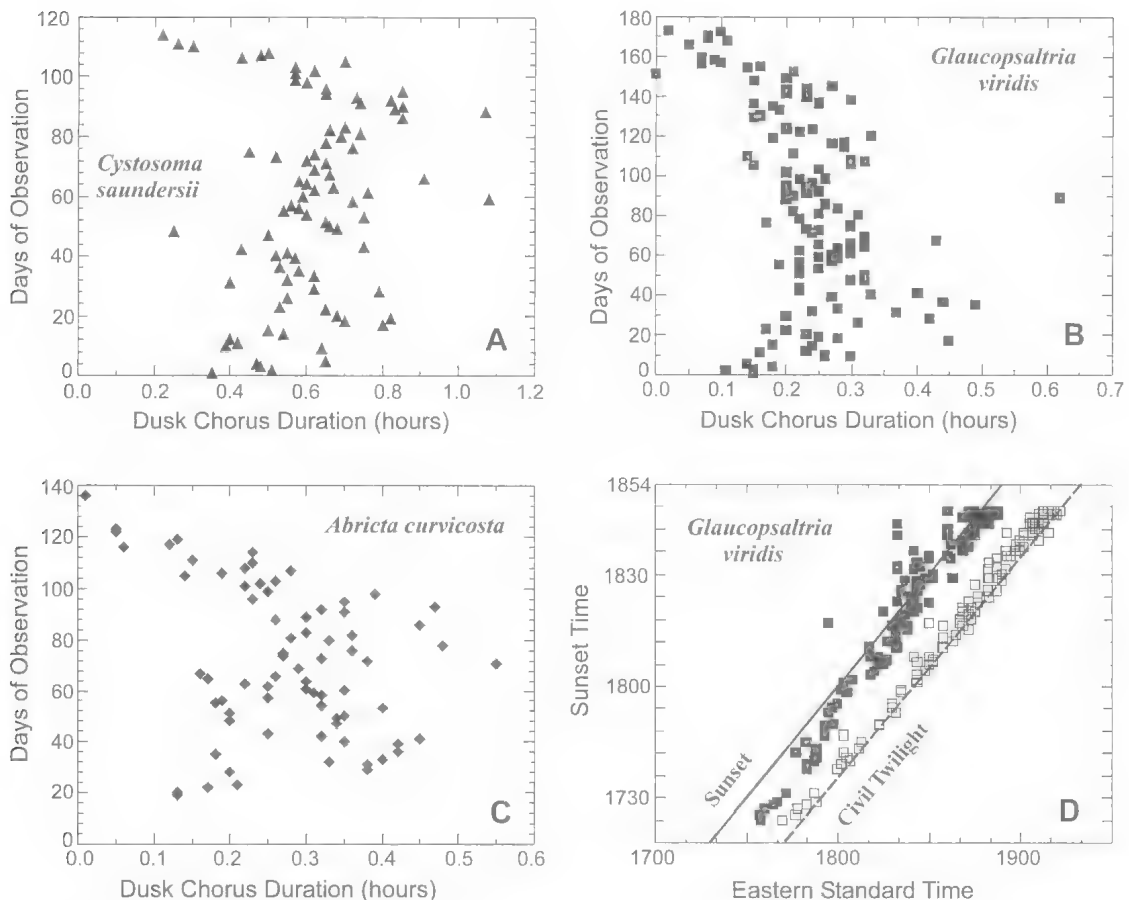


FIG. 7. A-C, dusk chorus duration in relation to progress of season (days of observation starting on 1 Nov, 1996, as in Figs 4 to 6). D, linear plot of sunset and twilight times in relation to the start/finish (filled/hollow symbols) of the dusk chorus of *G. viridis* over 6 month interval (as in Fig. 4).

duration and either start/finish T_a 's (r values of -0.20 to 0.28), or temperature gradients during choruses (r values 0.06 to 0.43); ii) although *A. curvica* and *C. saundersii* populations collapsed before those of the other 3 species, plots of days of observation (= season) versus T_a 's of chorus finish (\approx start) for both of these species show no corresponding late season decrease in T_a (e.g. Fig. 8B, illustrating the data for *C. saundersii*); iii) T_a data for *G. pluvialis* show late season decreases (Fig. 8C), yet no corresponding decrease in dusk chorus duration is found (although in this case, the subsurface micro-habitat is a complicating factor).

Synchrony: A high degree of synchrony occurs between the 6 insect species during dusk chorusing (Figs 3-6). A general time progression occurs from *T. tristigma* to *G. viridis*, *A.*

curvica (+ *P. claripennis*) to *G. pluvialis*, (Fig. 9). Mean chorus duration (Table 1) ranges from 0.29 (*A. curvica*) to 0.87 hour (*G. pluvialis*), which are consistent with dusk chorusing observations in Malaysian and Bornean rainforests (Gogola & Riede, 1995). Only the pre-sunset part of the *T. tristigma* song and the later part of the *G. pluvialis* chorus do not overlap with competing insect songs. The late afternoon to early evening period is an acoustically 'busy' period of the day, from spring through to autumn, particularly as birds are also acoustically active during the same time period. This implies that the temporal structures and frequencies of the songs of the respective insects are sufficiently species specific to enable mate recognition to occur, as further outlined below.

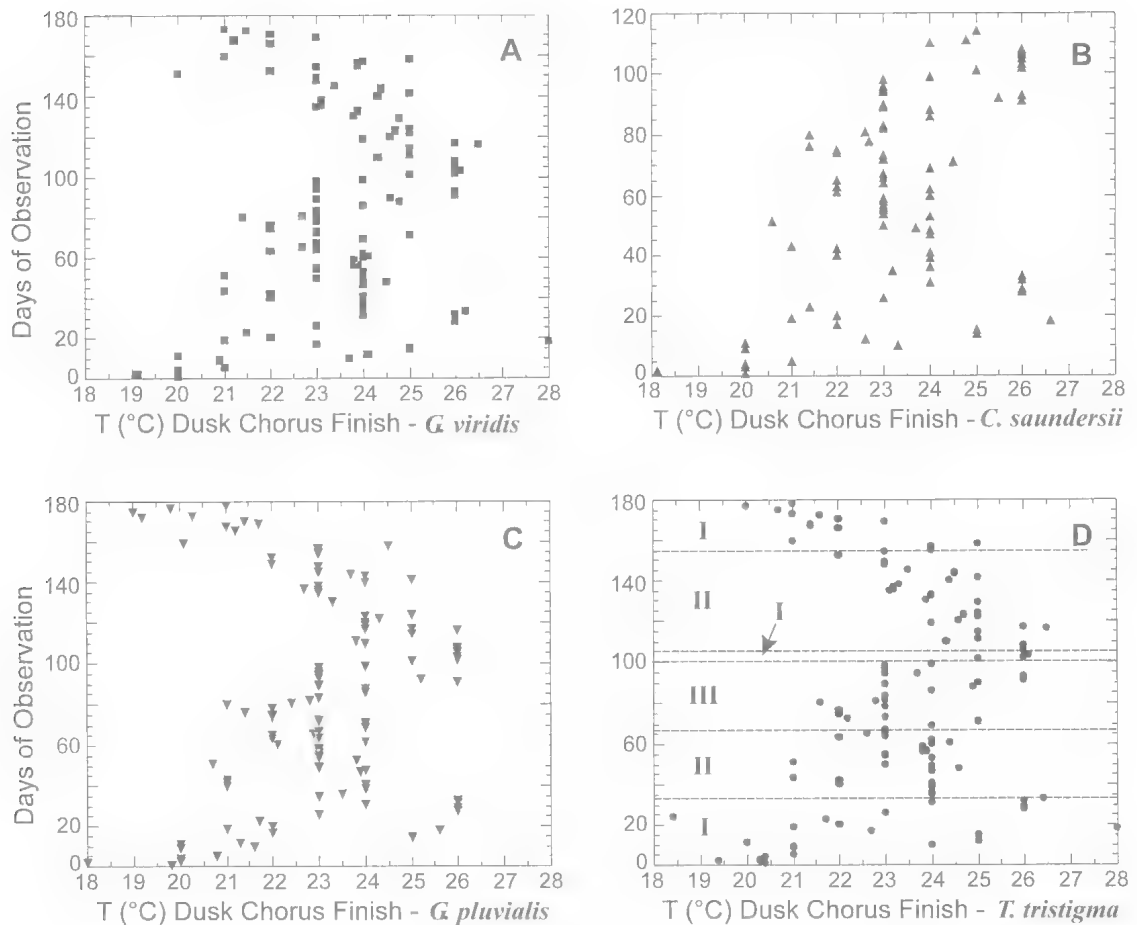


FIG. 8. Seasonal (days of observation) variation of ambient temperatures (T_a) at the cessation of dusk chorusing for: A, *G. viridis* (Fig. 4); B, *C. saundersii* (Fig. 4); C, *G. pluvialis* (Fig. 5); and D, *T. tristigma*. In (D) the phases of changing singing behaviour are shown, based on Fig. 6, as follows: I, discrete dusk chorusing; II, continuous afternoon singing through to dusk, with marked intensity increase near sunset; III, continuous song through to dusk, with no change in song intensity.

DISCUSSION

Henwood & Fabrick (1979) highlighted, with particular reference to vertebrates, the optimal acoustic environment provided within the dawn chorus window, e.g. reduced temperature gradients, low wind and wind gradients, and low abiotic noise. This is expected to lead to more efficient broadcast coverage and therefore significant advantages to individuals selecting the early morning calling environment. Young (1981) pointed out that the same data indicate that dusk is also a time of low background noise and relatively stable wind and temperature gradients

and again may lead to an adaptive advantage towards dusk chorusing.

The underlying reasons for dusk/dawn chorusing in many cicadas are still unknown, but the following points are relevant to the phenomenon: i) Not all cicadas exhibit such behaviour, which seems to be most prevalent in more localised (static) species with continuous/monotonous calls. Dusk/dawn chorusing may not occur in smaller species (e.g. some *Pauropsalta*) due to more rapid heat loss once solar radiation ceases, thereby causing body temperatures (T_b) to drop below the critical levels needed for song production (Sanborn, 1977). ii) Excepting crepuscular species, dawn/dusk chorusing

TABLE 2. Monthly mean ambient temperatures (T_a), temperature gradients during dusk chorus (start to finish), chorus duration's and chorus starts relative to sunset (SS). Data presented as means and standard deviations (in parentheses).

	November 1996	December 1996	January 1997	February 1997	March 1997	April 1997
<i>T. tristigma</i>						
Start T_a (°C)	23.6 (3.0)	24.1 (1.4)	24.2 (1.3)	25.8 (1.1)	24.8 (0.8)	22.8 (1.3)
Finish T_a (°C)	22.5 (2.6)	23.7 (1.2)	23.3 (1.3)	25.0 (1.2)	24.0 (0.8)	22.2 (1.4)
Temperature gradient	1.0 (1.4)	0.4 (0.5)	0.8 (0.6)	0.9 (0.6)	0.8 (0.5)	0.6 (0.6)
Chorus duration (hr)	0.53 (0.17)	0.75 (0.14)	1.79 (0.51)	1.49 (0.57)	0.77 (0.37)	0.44 (0.10)
(Chorus finish - SS) (hr)	0.28 (0.08)	0.30 (0.08)	0.33 (0.05)	0.33 (0.06)	0.36 (0.02)	0.30 (0.06)
n	20	24	24	20	17	16
<i>A. curvicauda</i>						
Start T_a (°C)	23.3 (2.3)	23.7 (1.3)	23.5 (1.2)	25.0 (1.2)	24.5 (0.9)	-
Finish T_a (°C)	23.2 (2.4)	23.5 (1.2)	23.2 (1.2)	24.9 (1.2)	24.4 (0.9)	-
Temperature gradient	0.5 (0.1)	0.2 (0.3)	0.3 (0.5)	(0.2)	(0.1)	-
Chorus duration (hr)	0.20 (0.09)	0.31 (0.08)	0.35 (0.17)	0.24 (0.10)	0.04 (0.02)	-
(Chorus start - SS) (hr)	0.31 (0.05)	0.23 (0.09)	0.21 (0.07)	0.26 (0.10)	0.20 (0.09)	-
n	6	24	24	19	3	-
<i>G. viridis</i>						
Start T_a (°C)	23.2 (2.7)	23.8 (1.3)	23.5 (1.2)	25.1 (1.2)	24.1 (1.3)	22.7 (1.3)
Finish T_a (°C)	22.6 (2.5)	23.6 (1.2)	23.3 (1.2)	24.9 (1.2)	23.7 (1.2)	22.6 (1.3)
Temperature gradient	0.6 (0.7)	0.2 (0.3)	0.2 (0.2)	0.2 (0.3)	0.4 (0.3)	0.2 (0.2)
Chorus duration (hr)	0.33 (0.09)	0.39 (0.07)	0.38 (0.09)	0.34 (0.05)	0.30 (0.06)	0.20 (0.05)
(Chorus start - SS) (hr)	0.04 (0.11)	-0.03 (0.11)	0.00 (0.11)	0.01 (0.07)	0.09 (0.04)	0.16 (0.04)
n	21	25	24	20	18	13
<i>C. saundersii</i>						
Start T_a (°C)	22.8 (2.6)	23.7 (1.3)	23.4 (1.2)	24.9 (1.2)	-	-
Finish T_a (°C)	22.3 (2.4)	23.3 (1.3)	23.1 (1.1)	24.8 (1.3)	-	-
Temperature gradient	0.5 (0.8)	0.4 (0.6)	0.3 (0.5)	0.1 (0.2)	-	-
Chorus duration (hr)	0.57 (0.14)	0.60 (0.15)	0.70 (0.13)	0.54 (0.17)	-	-
(Chorus start - SS) (hr)	0.26 (0.06)	0.27 (0.07)	0.26 (0.05)	0.26 (0.08)	-	-
n	20	24	24	16	-	-
<i>G. pluvialis</i>						
Start T_a (°C)	23.1 (2.7)	23.7 (1.3)	23.4 (1.3)	24.8 (1.2)	23.9 (0.8)	22.1 (1.5)
Finish T_a (°C)	22.0 (2.4)	23.1 (1.4)	23.0 (1.2)	24.6 (1.2)	23.5 (0.8)	21.5 (1.5)
Temperature gradient	1.1 (1.7)	0.6 (0.6)	0.4 (0.5)	0.2 (0.5)	0.4 (0.3)	0.7 (0.6)
Chorus duration (hr)	1.07 (0.37)	1.00 (0.43)	0.81 (0.24)	0.71 (0.27)	0.81 (0.23)	0.75 (0.29)
(Chorus start - SS) (hr)	0.13 (0.29)	0.24 (0.24)	0.34 (0.16)	0.32 (0.17)	0.37 (0.07)	0.38 (0.08)
n	20	23	23	20	15	16

species produce their main singing periods during the day. iii) During dusk chorusing, cicadas commonly become active, undertaking frequent localised flights to nearby branches or trees. This is especially notable in ♀♀ of *C. saundersii*, corresponding to the period of crepuscular mating activity (Daws et al., 1997). iv) Although overlap of chorusing occurs, species differ in chorus start and finish times. This suggests differing response levels to critical external stimuli (e.g. light intensity) for each species, but these may be modified by differing micro-habitat niches (e.g. dense vs open foliage). v) *C. saundersii* (and apparently other crepuscular species) do not exhibit dawn chorusing. vi) The dusk song of the *T. tristigma* is indistinguishable from the day song, while in *G. viridis* the dusk song is an extended version of the very brief 'whistle' song sporadically emitted during the day. *A. curvicauda* has a continuous coarse dusk song, which is the extended equivalent of the longer phrase emitted as part of the day song. *P. claripennis* produces a

continuous rattling song (which forms a major, but not continuous part of the day song). The dusk choruses of all species are therefore emitted as continuous songs, irrespective of the structure of the day songs. vii) *T. tristigma* systematically changes its late afternoon to dusk calling behaviour through the season, which seems most plausibly related to seasonal temperature patterns. A very general correspondence does exist between the T_a and singing patterns (Fig. 8D), as for example, the occurrence of discrete dusk chorusing behaviour during the slightly cooler November and April periods. In contrast, the brief re-occurrence of this behaviour in early February seems to follow a sharp shift to higher T_a . Overall, however, the T_a 's occurring during and between the periods of changing behaviour extensively overlap, as reflected in the very similar monthly average T_a 's for chorusing (Table 2). Available data are therefore inconclusive as to the role of T_a in explaining the changing behaviour patterns, and imply influence of additional factors.

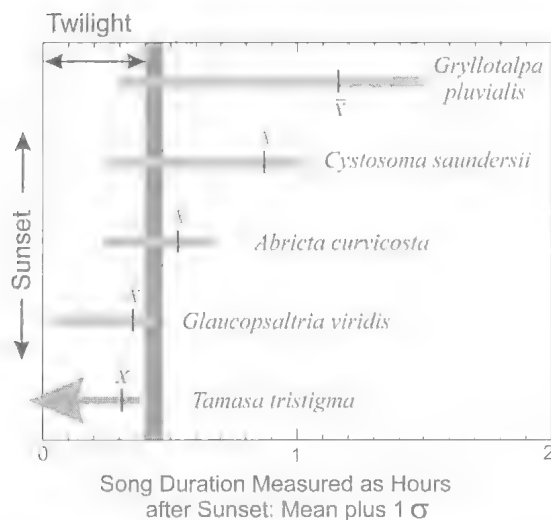


FIG. 9. Summary of dusk chorus duration, relative to sunset, of the five cicada and the mole cricket species. Twilight represents time between the sunset and civil twilight lines, the width of the civil twilight line marking the restricted seasonal variation of twilight through the observation period.

Staicer et al. (1996) listed 12 hypotheses in 3 categories to explain dawn/dusk chorusing in birds: 1) intrinsic to internal state, e.g. hormonal levels; 2) social function; 3) dawn preference resulting from daily timing of environmental selective pressures. Within these categories, the following aspects, in combination, are considered potentially relevant to cicadas:

1) Self-stimulation. Dawn chorusing perhaps represents a 'warming-up' strategy necessary for relatively static species (cf. Josephson & Young, 1979). A possible cue for dawn/dusk song could be the changing xylem-flow pressure within vegetation which stops at dusk and resumes at dawn, presumably responding to transpiration rate (e.g. Dolling, 1991:8). As noted, however, not all cicadas sing at dawn/dusk. 2) Mate attraction, certainly critical for dusk singing crepuscular insects. In other species, however, mating occurs throughout the day, with no observational evidence for unusually high mating activity at dawn/dusk. 3) Mate stimulation. The intensity of dawn/dusk chorusing, plus the optimal acoustic conditions, may facilitate female location of males at a time of lowered predation pressure. 4) Social dynamics. Chorusing may represent an effective mechanism, by signaling, of adjusting spatial distributions between calling males, after

dispersion during the day (e.g. by predation). Doolan & MacNally (1981) have shown that although aggregation is important in *C. saundersii* for increasing mating success, individuals space themselves at ~1-1.5m apart, with females selecting males only on the basis of their acoustic display. Doolan (1981) further suggests that the spatial distribution results from the interplay between selective pressures to aggregate (ensuring greater numbers of females), and selective pressure to space (enhancing individual success in mating). The short and intense dawn/dusk chorusing provides a mechanism for this to happen and explains the increased, but localised activity of individuals. It also may explain why chorusing is important for relatively localised and also for aggregating species. 5) Lowered predation rates from birds, reptiles, arachnids, and predatory insects. Doolan & MacNally (1981) note the more intense bird predation early in the dusk chorus of *C. saundersii*. 6) Acoustic transmission enhanced at dawn/dusk, as previously noted. 7) Energy reserves conserved/accumulated during night, stimulating burst of singing at dawn. This does not, however, explain the dusk chorus.

UNIQUENESS OF THE CICADA AND MOLE CRICKET SONGS. As noted, the extensive temporal overlap of songs during the acoustically 'busy' dusk window requires that the songs are species specific. A detailed presentation of the song characteristics is beyond the scope of this paper, but the essential temporal structures of the cicada songs are presented (as oscillograms/waveform plots) in Young (1972a,b; 1980), Simmons & Young (1978), Young & Josephson (1983) and Ewart (1995). The *G. pluvialis* call is documented by Otte & Alexander (1983). These data clearly show the distinctive temporal song structures of each species, seen in their pulse and phrase structures, and pulse repetition rates. The differences are also reflected in the dominant frequencies of the songs. For *G. viridis*, *C. saundersii*, *T. tristigma*, *A. curvicauda*, *P. claripennis* and *G. pluvialis*, these frequencies (author data) are, respectively (kHz): 1.8-1.9; 0.8-0.9; 6.1-8.4; 9.5-9.6; 5.9-6.8; and 2.1. Further differences are seen in the detailed structures of the frequency bands, i.e. whether broad or narrow, indicating the 'purity' of the emitted tones. These are represented as bandwidths, based on the sound energy emitted between the lower (25%) and upper (75%) quartiles determined from song spectra. Respective values are: 0.14; 0.28; 1.0; 2.3; 2.1; and 0.27kHz. The *G.*

viridis song closely approaches a modulated pure tone (see also Young & Josephson, 1983), while the songs of *G. viridis* and *G. pluvialis* exhibit well defined harmonics (to 5f), giving increased transmission flexibility to the songs.

Notwithstanding the extensive synchrony during dusk chorusing between species, the interspecific songs each have their uniquely defined acoustic properties.

ACKNOWLEDGEMENTS

I thank Geoff Monteith, Queensland Museum, for making numerous improvements to the manuscript and Dr M. Coombs for emphasising the potential importance of temperature in interpreting the data.

LITERATURE CITED

- BECK, S.D. 1980. Insect photoperiodism. 2nd edition. (Academic Press: New York, London).
- CRAWFORD, C.S. & DADONE, M.M. 1979. Onset of evening chorus in *Tibicen marginalis* (Homoptera: Cicadidae). *Environmental Entomology* 8(6): 1157-1160.
- DAWS, A.G., HENNIG, R.M. & YOUNG, D. 1997. Phonotaxis in the cicadas *Cystosoma saundersii* and *Cyclochila australasiae*. *Bioacoustics* 7(3): 173-188.
- DOLLING, W.R. 1991. The Hemiptera. (Oxford University Press: Oxford).
- DOOLAN, J.M. 1981. Male spacing and the influence of female courtship behaviour in the bladder cicada, *Cystosoma saundersii* Westwood. *Behavioral Ecology and Sociobiology* 9: 269-276.
- DOOLAN, J.M. & MACNALLY, R.C. 1981. Spatial dynamics and breeding ecology in the cicada *Cystosoma saundersii*: The interaction between distributions of resources and intraspecific behaviour. *Journal of Animal Ecology* 50: 925-940.
- DUFFELS, J.P. 1988. The cicadas of the Fiji, Samoa and Tonga Islands, their taxonomy and biogeography (Homoptera, Cicadoidea). *Entomonograph* 10. (E.J. Brill/Scandinavian Science Press).
- ENDLER, J.A. 1992. Signals, signal conditions, and the direction of evolution. *The American Naturalist* 139 (Supplement): S125-S153.
- EWART, A. 1989. Revisionary notes on the genus *Pauropsalta* Goding and Froggatt (Homoptera: Cicadidae) with special reference to Queensland. *Memoirs of the Queensland Museum* 27(2): 289-375.
1995. Cicadas. Pp. 79-88. In Ryan, M. (ed.) *Wildlife of Greater Brisbane*. (Queensland Museum: Brisbane).
- GOGALA, M. 1995. Songs of four cicada species from Thailand. *Bioacoustics* 6: 101-116.
- GOGALA, M. & RIEDE, K. 1995. Time sharing of song activity by cicadas in Temengor Forest Reserve, Hulu Perak, and in Sabah, Malaysia. *Malayan Nature Journal* 48: 297-305.
- HENWOOD, K. & FABRICK, A. 1979. A quantitative analysis of the dawn chorus: Temporal selection for communicatory optimization. *The American Naturalist* 114(2): 260-274.
- JOSEPHSON, R.K. & YOUNG, D. 1979. Body temperature and singing in the Bladder Cicada, *Cystosoma saundersii*. *Journal of Experimental Biology* 80: 69-81.
- MOORE, T.E. 1962. Acoustical behavior of the cicada *Fidicina pronoe* (Walker) (Homoptera: Cicadidae). *Ohio Journal of Science* 62: 113-119.
- MYERS, J.G. 1929. *Insect singers*. A natural history of the cicadas. (George Routledge & Sons: London).
- NIELSEN, E.T. 1963. Illumination at twilight. *Oikos* 14(1): 9-21.
- OTTE, D. & ALEXANDER, R.D. 1983. The Australian crickets (Orthoptera: Gryllidae). *Academy of Natural Sciences of Philadelphia Monograph* 22.
- RIEDE, K. 1996. Diversity of sound-producing insects in a Bornean lowland rain forest. Pp. 77-84. In Edwards, D.S. et al. (eds) *Tropical Rainforest Research - Current Issues*. (Kluwer Academic Publishers: Netherlands).
1997. Bioacoustic monitoring of insect communities in a Bornean rainforest canopy. Pp. 442-452. In Stork, N.E., Adis, J. & Didham, R.K. (eds) *Canopy Arthropods*. (Chapman & Hall: London).
- RIEDE, K. & KROKER, A. 1995. Bioacoustics and niche differentiation in two cicada species from Bornean lowland forest. *Zoologischer Anzeiger* 234: 43-51.
- SANBORN, A.F. 1997. Thermal biology of cicadas (Homoptera: Cicadoidea). *Trends in Entomology* 1: 89-104.
2000. Comparative thermoregulation of sympatric endothermic and ectothermic cicadas (Homoptera: Cicadidae: *Tibicen winnemanna* and *Tibicen chloromerus*). *Journal of Comparative Physiology A* 186: 551-556.
- SIMMONS, P. & YOUNG, D. 1978. The tymbal mechanism and song patterns of the bladder cicada, *Cystosoma saundersii*. *Journal of Experimental Biology* 76: 27-45.
- STAICER, C.A., SPECTOR, D.A. & HORN, A.G. 1996. The dawn chorus and other diel patterns in acoustic signaling. Pp. 426-453. In Kroodsma, D.E. & Miller, E.H. (eds) *Ecology and evolution of acoustic communication in birds*. (Cornell University Press: Ithaca, London).
- YOUNG, A.M. 1976. Notes on the faunistic complexity of cicadas (Homoptera: Cicadidae) in northern Costa Rica. *Revista de Biología Tropical* 24: 267-279.
1981. Temporal selection for communicatory optimization: The dawn-dusk chorus as an

- adaptation in tropical cicadas. The American Naturalist 117: 826-829.
1982. Population Biology of Tropical Insects. (Plenum: New York, London).
- YOUNG, D. 1972a. Neuromuscular mechanism of sound production in Australian cicadas. Journal of Comparative Physiology 79: 343-362.
- 1972b. Analysis of songs of some Australian cicadas (*Homoptera: Cicadidae*). Journal of the Australian Entomological Society 11: 237-243.
1980. The calling song of the Bladder Cicada *Cystosoma saundersii*: A computer analysis. Journal of Experimental Biology 88: 407-411.
- YOUNG, D. & JOSEPHSON, R.K. 1983. Mechanisms of sound-production and muscle contraction kinetics in cicadas. Journal of Comparative Physiology 152: 183-195.

PLATYHELMINTHES FROM SALT MARSHES OF COOMERA RIVER, SOUTHEASTERN QUEENSLAND, AUSTRALIA

ANNO FAUBEL AND BRONWYN CAMERON

Faubel, A. & Cameron, B. 2001 06 30: Turbellaria from salt marshes of Coomera River, southeastern Queensland, Australia. *Memoirs of the Queensland Museum* 46(2): 511-519. Brisbane. ISSN 0079-8835.

Three new species, *Childanea coomerensis* gen. et sp. nov. (Acoela), *Macrostomum greenwoodi* sp. nov. and *Macrostomum coomerensis* sp. nov. (Macrostomida) are described from the brackish water estuarine area of the Coomera river, Gold Coast, Queensland, Australia. □ *Taxonomy, morphology, flatworms, Acoela, Macrostomida.*

Dr A. Faubel, Institut für Hydrobiologie und Fischereiwissenschaft, Universität Hamburg, Zeiseweg 9, D-22765 Hamburg, Germany (e-mail: faubel@uni-hamburg.de); B. Cameron, The University of Queensland, St Lucia 4072, Australia; 14 March 2000.

The Australian fauna of Acoela and Macrostomida of limnetic, brackish and marine habitats is not very well known. Over a long time the only study known on Acoela was carried out by Haswell (1905) on *Heterochaerus australis*. More recently, however, more intensive studies have been started by Trench & Winsor 1987 on *Amphiscolops* sp. and *Haplodiscus* sp. (in part *Waminoa litus* Winsor, 1990), Winsor 1988 on *Wulguru cuspidata*, Winsor 1990 on *Convolutriloba hastifera*, *Waminoa litus*, *W.* sp. 1, and *W.* sp. 2.

A first census of macrostomid species of Australia by Faubel et al. (1994) listed 6 species. Of these *Macrostomum tuba* v. Graff, 1882 and *Promacrostomum palum* Sluys, 1986 are known from freshwater environments. *Dunwichia arenosa* Faubel, Blome & Cannon, 1994, *Bradburia australiensis* Faubel, Blome & Cannon, 1994, *Macrostomum australiense* Faubel, Blome & Cannon, 1994, and *Macrostomum* sp. Faubel, Blome & Cannon, 1994, however, are all known from eulittoral habitats of sandy beaches of Stradbroke Island, South Queensland.

In the present paper one acoelous species and two macrostomid species from brackish water habitats are described.

METHODS

For studies on meiobenthos, sediment was qualitatively collected from the Coomera salt-marsh pools. The freshly collected sediment was transferred into a glass tank in a constant temperature room approximating ambient conditions (Salinity ca 30 ppt, 27°C). Habitat water was added to the sediment tank, to a depth of about 15cm. A series of 60 watt light bulbs

were suspended above the tank to attract organisms into the water column. Every hour, the tank was siphoned through a 63µm sieve to collect emerged fauna. The defaunated water was then returned to the tank and the extraction process repeated until the majority of the organisms had been collected. Sexually mature specimens of Turbellaria were studied alive and in squash preparation, i.e. flattened under the increasing pressure of the coverslip as the preparation dried. Measurements of living organisms (m.l.s.) were made from squashed ones. These measurements are given in parentheses in the running text. All other measurements were made from sections of the holotype. For histological observation specimens were relaxed in 7% MgCl₂ and fixed in Bouin's fixative. Specimens were embedded in Paraplast plus (Reichert & Junk) and cut sagittally at 3.0µm and stained with haematoxylin-eosin according to Mayer. Types are deposited in the Queensland Museum, Brisbane.

SITE DESCRIPTION

Coomera salt-marsh (27°54'S, 153°17'E) was chosen as a site for turbellarian collection. For the past 4 years this site had been excluded from the broad-scale mosquito control measures that typically occur in southeast Queensland. It was therefore considered to be a relatively pristine site.

Coomera salt-marsh is only inundated by tides of 2.4m or more above datum. Salinity ranges between 25-38 ppt. The salt-marsh pools are 2-7m² in area and are bordered by dense clumps of *Sporobolus virginicus* (Kunth.) the dominant marsh-grass, and *Sarcocornia quinqueflora* Bunge (ex. Ung. Stern) a sprawling herbaceous

halophyte. The sediment consists of much highly organic mud with negligible amounts of sand.

SYSTEMATICS

Order ACOELA Uljanin, 1870
Family CHILDIIDAE Dörjes, 1968

Childiane gen. nov.

DIAGNOSIS. Childiidae with frontal organ. Body wall musculature with outer circular and inner longitudinal muscle fibers. Separate genital openings. Seminal bursa with vagina and cellular bursa mouth directed anteriad. Paired ovaries and testes. Male copulatory apparatus without seminal vesicle; proximal ejaculatory duct with sclerotised layer working as penial stylet; distal ejaculatory duct with prostatic glands. False seminal vesicles present.

TYPE SPECIES. *Childiane coomerensis* sp. nov.

ETYMOLOGY. Derived from the generic name *Childia*.

KEY TO THE GENERA OF THE CHILDIIDAE

1. with single male copulatory organ 3
 - with several male copulatory organs 2
2. with 2 male copulatory organs . . . *Childia* v. Graff, 1910
 - with 4 male copulatory organs *Tetraposthia* An Der Lan, 1936
- 3(1). . . with single male copulatory organ; without seminal bursa 4
 - with seminal bursa 6
4. without male atrium or very short 5
 - with long male atrium *Atriofronta* Dörjes, 1968
5. copulatory organ with sclerotised spines
 - *Actinoposthia* An Der Lan, 1936
 - copulatory organ with rosette like muscular elements encasing the seminal vesicle *Paraproporus* Westblad, 1945
- 6(3). with seminal bursa; body muscle wall with outer circular and inner longitudinal muscle fibers. 7
 - body muscle wall with inverse muscle layers *Paraphanostoma* Steinböck, 1931
- 7 with bursa nozzle. 8
 - without bursa nozzle . . . *Pseudactinoposthia* Dörjes, 1968
8. bursa nozzle directed anteriad or caudad 9
 - bursa nozzle invaginated in the seminal bursa *Pelophila* Dörjes, 1968
9. bursa nozzle cellular 10
 - bursa nozzle sclerotised . . . *Philactinoposthia* Dörjes, 1968
10. male complex with prostatic glands, without seminal vesicle *Childiane* gen. nov.
 - male complex with seminal vesicle, without prostatic glands. *Archactinoposthia* Dörjes, 1968

Childiane coomerensis sp. nov. (Figs 1A-B, 2)

ETYMOLOGY. From the Coomera River estuary on the Gold Coast of Queensland.

MATERIAL, HOLOTYPE. Coomera salt-marsh (27° 4'S, 153° 17'E), Gold Coast, southeast Queensland, QM G217362, 2 specimens, May 1998 leg. B. Cameron.

DESCRIPTION. Length of body of living sexually mature specimens up to 0.9mm, when extended and gliding; maximum width up to 0.18mm in second half of body, area of growing oocytes. Body spindle-shaped with rounded frontal and rear body end, dorso-ventrally flattened. Posterior body end with a small vacuole being horseshoe-like (Fig. 1A). In transmitted light, colour of body yellowish but digestive parenchyme and lumen bright yellow through ingested diatoms. Glandular ducts of frontal organ open to exterior through several pores at the frontal end, the glands of which lie posterior to the statocyst. Secretion of the glands coarsely granulated. Statocyst embedded within the medio-frontal brain, about 55µm (m.l.s.) distant from anterior body end. Epidermal cells 2.0 - 2.5µm high, with intraepithelial nuclei; rhabdoids lacking. Epidermis completely covered with cilia 3.5 - 4.0µm in length. Body wall musculature with faint outer circular and inner longitudinal fibers. Dorsal and ventral subepidermal hyaline glands open to the exterior throughout body surface, more abundant lateral. Digestive lumen bordered by nucleus-rich parenchymal tissue which starts immediately at level of frontal glands and fills the whole mid-body covering the ovaries dorsal. Gut lumen filled with diatoms and detritus. Mouth ventral behind mid-body, about 400µm (m.l.s.) distant from frontal body end.

Reproductive system (Fig. 2). Lateral testes situated about 180µm (m.l.s.) from anterior body end. Spermatids penetrate the parenchyma on both sides lateral of the ovaries. Anterior to the transverse level of the male complex the spermatids accumulate in two false seminal vesicles which enter the common proximal ejaculatory duct in common. True seminal vesicle lacking. Ejaculatory duct is closed by a sphincter at junction of the vasa deferentia. The ventral male pore (Fig. 1B,2), 32µm distant from rear body end, leads to the bulbous pyriform copulatory organ. Muscle bulb a highly muscular complex 43µm in length with central ejaculatory duct (Fig. 2). The muscle fibers run more or less

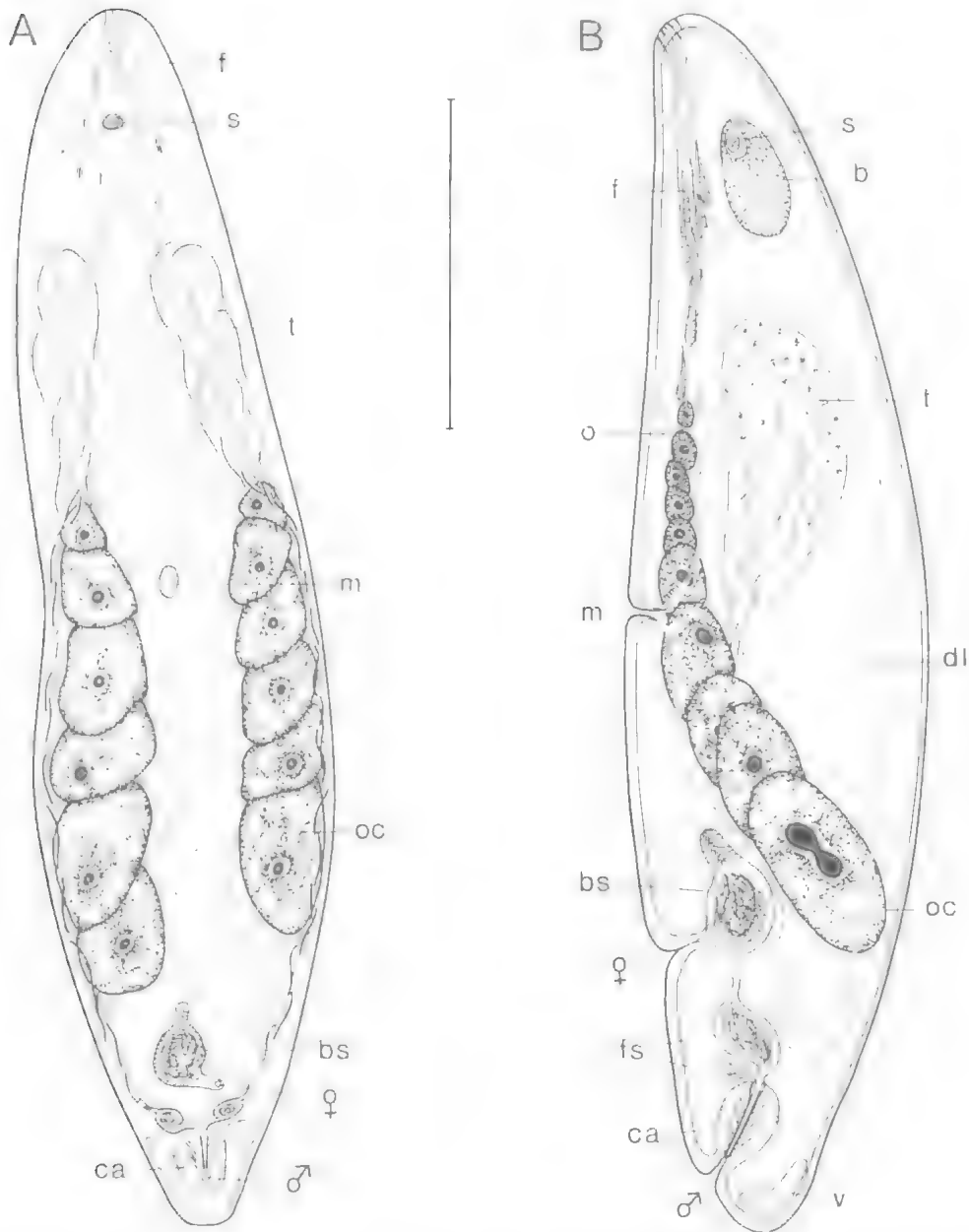


FIG. 1. *Childianca coomerensis*, gen. et sp. nov. A, dorsal view in squash preparation. B, diagrammatic sagittal reconstruction after serial sections. Scale: 200µm. (b = brain, bs = seminal bursa, bm = mouth of bursa, ca = copulatory apparatus, dl = digestive lumen, f = frontal organ, fs = false seminal vesicle, m = mouth, o = ovary, oc = oocyte, s = statocyst, t = testis, v = vacuole, ♂ = male gonopore, ♀ = female gonopore).

parallel, inclining toward the ejaculatory duct, and obviously function as retractors during copulation. Ejaculatory duct tripartite; proximal part of duct (Fig. 2) about 10µm long, highly sclerotised forming a seal controlling sperm ejaculation; central one, 31µm long, lined by a

sclerotised epithelial layer looking stylet-like; distal part is 12µm long, not ciliated, and of prostatic function. Cell bodies of epithelial layer very elongated, enclose copulatory complex (Fig. 2).

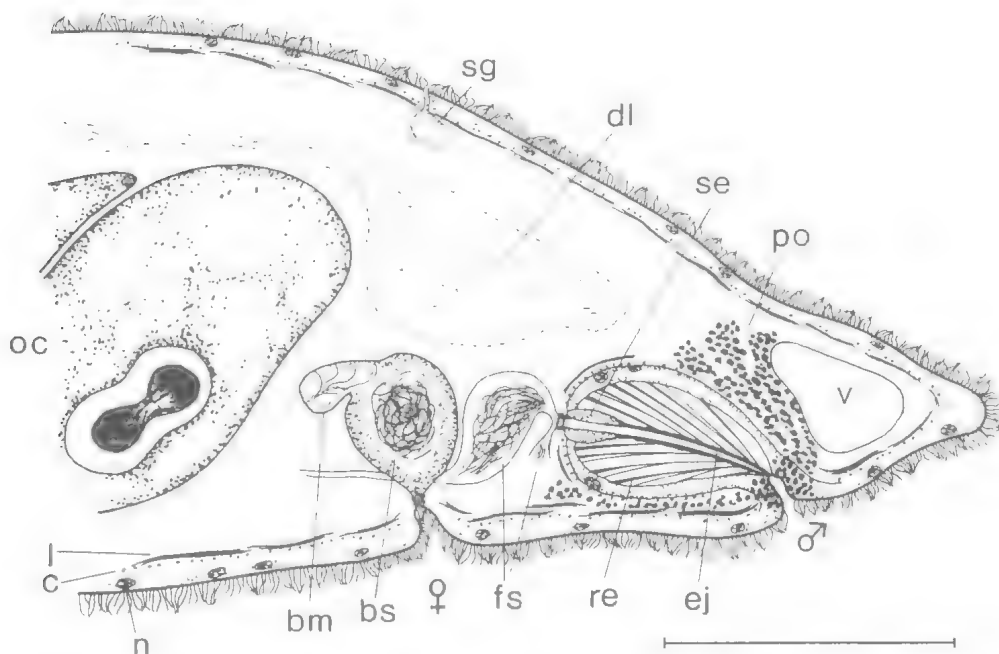


FIG. 2. *Childianeia coomerensis*, gen. et sp. nov.; sagittal reconstruction of the male and female complex. Scale: 50µm. (bs = seminal bursa, bm = mouth of bursa, c = circular muscles, dl = digestive lumen, ej = ejaculatory duct, fs = false seminal vesicle, l = longitudinal muscles, n = nucleus, oc = oocyte, po = prostatoid glands, re = retractor muscles, se = seal, sg = subepidermal gland, v = vacuole, ♂ = male gonopore, ♀ = female gonopore).

Female system with paired ovaries and a seminal bursa. Oogonia of each ovary lie ventro-lateral, 190–200µm behind statocyst (Fig. 1B). A line of growing oocytes runs latero-caudad. Hindmost oocytes are about 170µm (m.l.s.) distant from posterior body end. Seminal bursa with a distal ciliated atrium (7.5µm long), a central vesicle filled with sperm (20µm in diameter), and a cellular mouth piece 13µm long. The atrium rises dorsad, 65µm anterior to male pore, widening proximad to form a vesicle filled with sperm. The cellular bursa mouth piece is directed antieriad, reaching central the hindmost part of the oocytes. Aperture between atrium and vesicle of bursa is closed by a sphincter.

DIAGNOSIS. With characters of the genus.

DISCUSSION. The family Childiidae was established and discussed in detail by Dörjes 1968. Up to now the family contains 10 genera. Dörjes included in this family all these genera of Acoela which have species with a sclerotised (cuticular according to Dörjes 1968), muscular, or cellular penis plug which is never invaginated in the seminal vesicle. The new species *Childianeia coomerensis* is characterized by a sclerotised ejaculatory duct obviously working

as a pointed stylet. On the basis of this character the species belongs to the Childiidae. *Coomera coomerensis*, however, differs from all species of the known genera of the family Childiidae in the presence of prostatic glands entering the distal ejaculatory duct. In combination with the characters of presence of a seminal bursa with a cellular spermiducal duct directed frontad and absence of a true seminal vesicle, establishment of monotypic *Childianeia* and its species *C. coomerensis* sp. nov. is justified within the family Childiidae.

Order MACROSTOMIDA, Meixner, 1924
Family MACROSTOMIDAE Van Beneden,
1870

Macrostomum greenwoodi sp. nov.
(Fig. 3)

ETYMOLOGY. Named in honour of Prof. J. Greenwood, University of Queensland.

MATERIAL. HOLOTYPE. Coomera salt-marsh (27°54'S, 153°17'E), Gold Coast, southeast Queensland, QMG217363, 2 specimens, April 1998 leg. B. Cameron.

DESCRIPTION. Length of body of living sexually mature specimens up to 1.3mm, when

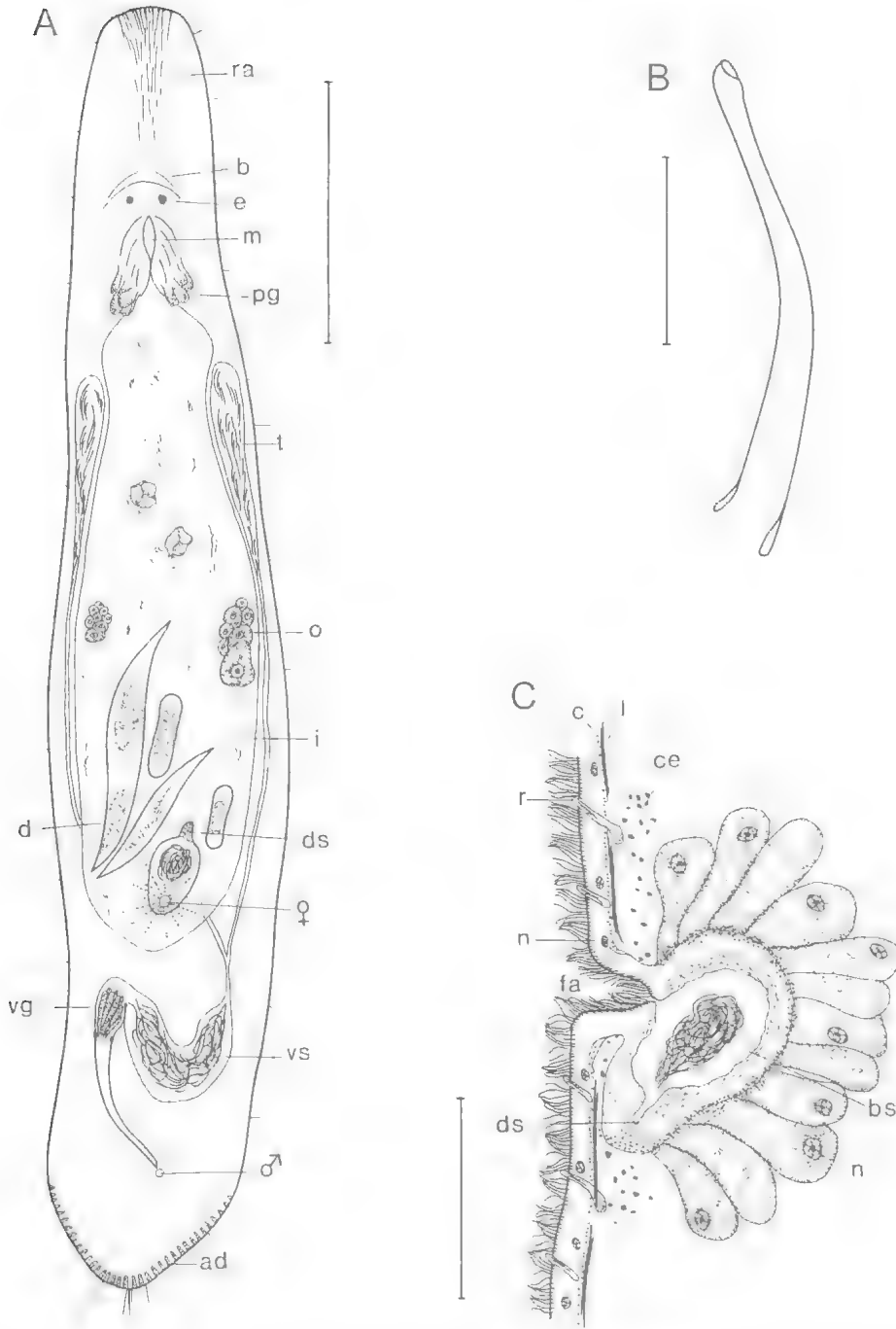


FIG. 3. *Macrostomum greenwoodi*, sp. nov. A, dorsal view in squash preparation. B, male stylet. C, sagittal reconstruction of the female organ. Scales: A, 200µm; B, 20µm; C, 50µm. (ad = adhesive glands, b = brain, bs = seminal bursa, c = circular muscles, ce = cement glands, d = diatoms, ds = spermiducal duct, e = eyes, fa = female atrium, i = intestine, l = longitudinal muscles, m = mouth, n = nucleus, o = ovary, pg = pharyngeal glands, r = rhabdite, ra = rhammites, t = testis, vg = vesicula granulorum, vs = seminal vesicle, ♂ = male gonopore. ♀ = female gonopore).

extended and gliding; maximum width up to 0.18mm in mid-body. Outline of body with characteristic macrostomid like anterior end; posterior end rounded, provided with strong adhesive glands (Fig. 3A). Around margin weak sensory hairs of varying length and stiffness present. In incident light body brownish with darker contrasting oocytes in the posterior part of body; gut intensively coloured yellow based on the uptake and consumption of bright yellow diatoms. Eyes present, 175µm (m.l.s.) far from anterior margin of the body. Crescentic brain 169µm (m.l.s.) distant from anterior end. Rhammite glands open ventro-frontal through the anterior margin of body, their cells extending posteriad up to the level of the pharynx simplex. In mid-body cells of epidermis 4.6µm high covered with 4.0 to 4.6µm (ventral) and 3.4 to 3.9µm (dorsal) long cilia. Intraepithelial nuclei present; rhabdites about 9.0µm long, the cell bodies of which subepidermal, up to 11.3µm long. Rhabdites distributed in longitudinal rows over the dorsal and ventral body surface. Body muscle wall with outer circular and inner longitudinal muscle fibers. Basal membrane not observed. Digestive system with pharynx simplex pierced by extrapharyngeal glands and large intestine but less numerous ciliated than pharynx. The intestine fills the median parts over the ovaries, oocytes, and seminal bursa and extends caudad up to the seminal vesicle. Mouth behind brain, 210µm (m.l.s.) distant from anterior end. The species feeds on diatoms and detritus particles. Ingested sand grains covered with detritus are abundant. Excretory system not observed, probably absent. Male and female gonopores separate, 185µm (m.l.s.) distant from each other.

Reproductive system (Fig. 3). The male system is typically macrostomid like. It consists of bilateral testes, vasa deferentia running caudad to either side of the intestine and ovaries, a common vas deferens, a seminal vesicle, a prostatic vesicle, and a male stylet which projects into the short male antrum. The stylet depicted in Fig. 3A, is 98.3µm long; the proximal opening is 12.0µm in diameter; the distal opening is subterminal. The male pore is 105µm (m.l.s.) distant from rear body end. The antrum rising dorsad is 10.8µm long.

The female system consists of bilateral ovaries and a seminal bursa. The ovaries forming lateral fields of oogonia, lie behind the germinative zone of the testes in mid-body (Fig. 3A), generating caudad large oocytes. The seminal bursa consists

of a ciliated atrium (11.4µm long), a bursal vesicle (37.9µm long), and a spermatid duct (12.8µm long). The bursal vesicle is totally lined with elongated cells. The proper epithelium of the bursa looks syncytially in which the surrounding cells (up to 35µm) excrete obviously coarsely granulated secretion. Cement glands surrounding the female pore, discharge their secretion into the female atrium.

DIAGNOSIS. The species is diagnosed on the outline of the male stylet (Fig. 3B).

***Macrostomum coomerensis* sp. nov.**
(Fig. 4)

ETYMOLOGY. From the Coomera river of the Gold Coast of Queensland.

MATERIAL. HOLOTYPE. Coomera salt-marsh (27°54'S, 153°17'E), Gold Coast, southeast Queensland, QM G217364, 2 PARATYPES. Same data, QM G217365-366, numerous specimens, April 1998 leg. B. Cameron.

DESCRIPTION. Length of body of living sexually mature specimens up to 1.4mm, when extended and gliding; maximum width up to 0.25mm in anterior part of second body-half, area of oocytes (Fig. 4A). Anterior and posterior body end rounded. Marginal hairs or spines absent. Frontal glands present, not reaching anterior level of brain. Eyes present immediately behind crescentic brain, 125µm (m.l.s.) distant from anterior margin of body. In incident light colour brownish yellow with contrasting darker lateral ovaries. In transmitted light body greyish translucent with yellowish digestive system. Mouth opening immediately caudal of eyes. From mouth the pharynx simplex rises dorso-caudad and receives openings of digestive glands. Intestine with less numerous cilia. The gut fills the median parts of the body extending caudad over ovaries and oocytes, ending up at the anterior level of the last oocytes. Rhabdites evenly distributed in serial lines over the body. Ventral rhabdites 7.5µm and dorsal ones 9.4µm long. Rear dorsal body end with dense aggregates of large rhabdites (10.7µm long). Ventral epidermis is 5.7µm thick and dorsal one is 2.8µm thick, entirely covered with 5.7µm long cilia; epithelial nuclei subepidermal. Basal membrane not observed. Body muscle wall with outer circular and inner longitudinal muscle fibers. Excretory system not observed, probably absent. Gonopores separate, 65µm distant from each other. Bilateral testes anterior to ovaries; last in mid-body.

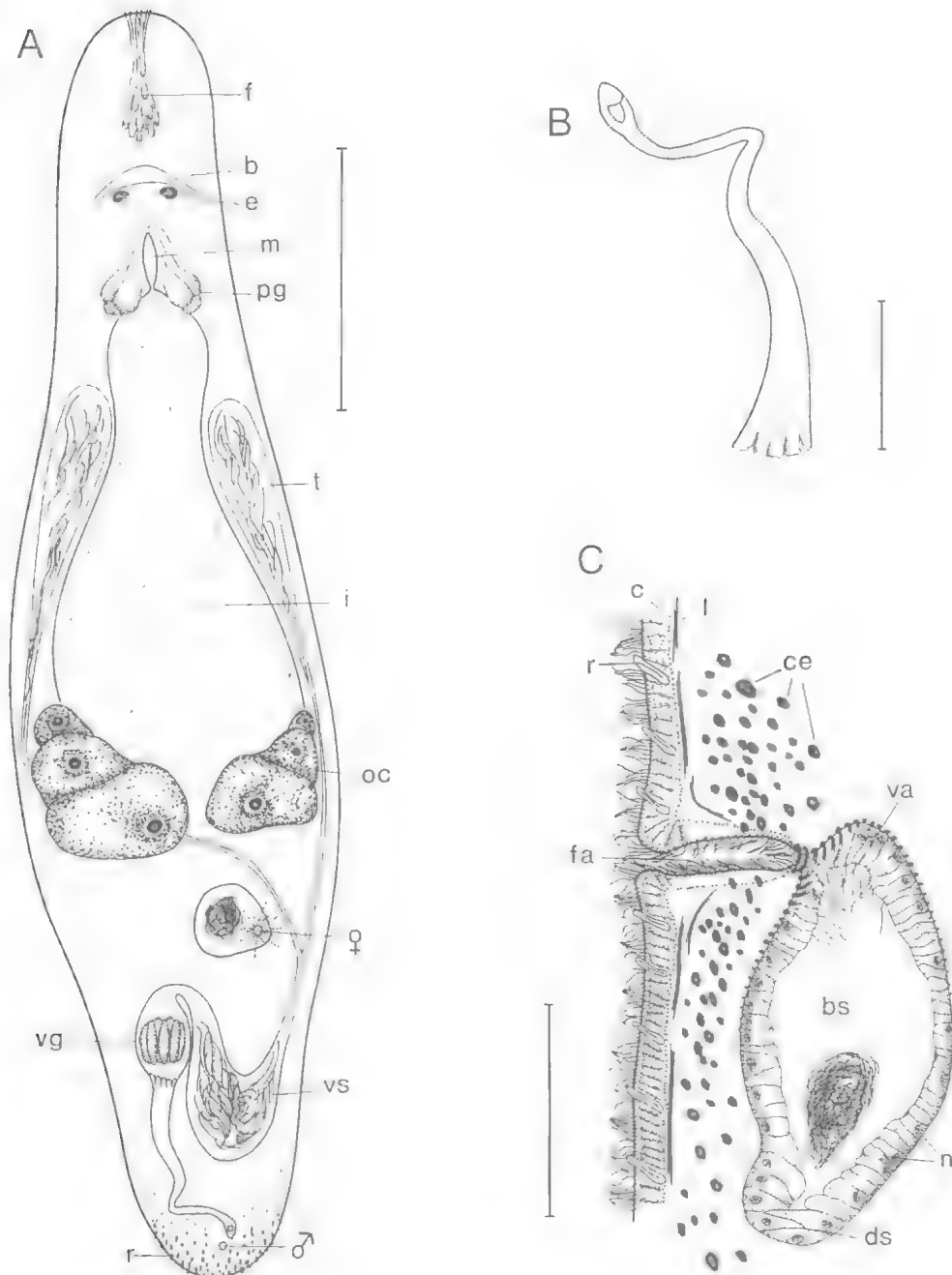


FIG. 4. *Macrostomum coomerensis*, sp. nov.; A, dorsal view in squash preparation. B, male stylet. C, sagittal reconstruction of the female organ. Scales: A, 200 μ m; B, C, 50 μ m. (b = brain, bs = seminal bursa, c = circular muscles, ce = cement glands, ds = spermiducal duct, e = eyes, f = frontal organ, fa = female atrium, i = intestine, l = longitudinal muscles, m = mouth, n = nucleus, o = ovary, pg = pharyngeal glands, r = rhabdite, t = testis, va = vagina, vg = vesicula granulorum, vs = seminal vesicle, σ = male gonopore, φ = female gonopore).

Reproductive system (Fig. 4). The male system is typically macrostomid like. It consists of bilateral

testes, vasa deferentia running caudad to either side of the intestine and ovaries, a common vas

deferens, a seminal vesicle, a prostatic vesicle, and a male stylet which projects into the male antrum. The sac-like testes are located 100 to 110 μm (m.l.s.) behind the pharynx. Latero-caudal of the female bursa the vasa deferentia unite to a common vas deferens on the left side before entering the seminal vesicle. The distal part of the seminal vesicle, the prostatic vesicle, and the proximal part of the penial sheath in which the stylet rests, are covered with a complicated system of strong muscle fibers. These fibers are responsible for protrusion and retraction of the stylet and ejaculation of sperm into the female system. The distal part of the prostatic vesicle is encased in the proximal portion of the stylet being slightly funnel-like extended. The stylet is 125 μm (m.l.s.) long; the distal two thirds are spiralled as outlined in Fig. 4B. The distal tip of the stylet is broadend, the opening of which lies subterminally. The male pore, 42.7 μm distant from the rear body end leads antero-dorsad to a rather long male antrum (15.2 μm).

The female system consists of bilateral ovaries and a seminal bursa. The oögonia generate laterally immediately behind the testes and are growing up caudad forming oocytes on each side of the body. The female genital pore is 280 μm (m.l.s.) distant from the caudal body end. The female atrium (43.5 μm long) entered by cement glands, is outlined with cilia and rises dorsad. The transition to the vagina is closed by a sphincter. The vagina, up to 31.5 μm long, ciliated, extends frontad to form a bursal vesicle filled with sperm. The cilia of the vagina up to 13.0 μm long. Anteriad of the bursa a spermiducal duct (24 μm long) is present. The spermiducal duct reaches up mediad to the level of the last oocytes. The epithelia of the vagina, the bursal vesicle, and the spermiducal duct are cellular with intraepithelial nuclei.

DIAGNOSIS. The species is diagnosed on the outline of the male stylet (Fig. 4).

DISCUSSION. Macrostromidae currently contains 11 genera. The dominant taxonomic characters concern the male copulatory apparatus: a distally armed ejaculatory duct (stylet), or an unarmed cirrus. Genera having a penial stylet are *Macrostromum* Schmidt, 1848, *Omalostomum* Van Beneden, 1870, *Promacrostromum* An Der Lan, 1939, *Archimacrostromum* Ferguson, 1954, *Bradynectes* Rieger, 1971, and *Bradburia* Faubel, Blome & Cannon, 1994. Of these genera, *Macrostromum* has the most species (127).

Beklemishev (1951) has assigned the species of *Macrostromum* to 3 taxonomic groups as follows: *Macrostromum hystricinum* group (stylets being funnel-like proximally, with tapered hook-like shape distally), *Macrostromum orthostylum* group (stylets being straight or curved, distad evenly tapering), and *Macrostromum tuba* group (stylets having a distal characteristic *Macrostromum tuba*-like enlargement, with the opening of the ejaculatory duct in the centre of the tip, or subterminally). Although these groupings are useful in a taxonomic sense, they should not be regarded as phyletic groupings because there are different lines of the development of the female genital organs within each group. A revision of the taxon Macrostromida is in preparation by the first author. Based on the distal features of the stylet, *Macrostromum coomerensis* belongs to the *Macrostromum tuba* group and *Macrostromum greenwoodi* to the *Macrostromum orthostylum* group.

Macrostromum coomerensis is characterised by having the male stylet formed like a cork-screw with a distal enlargement, and a subterminal opening of the ejaculatory duct. On the basis of these features the species belongs to the *Macrostromum tuba* group. *Macrostromum* species with a spiral stylet are: *M. leptos* An Der Lan, 1939, *M. lewisi* Ferguson, 1939, *M. reynoldsi* Ferguson, 1939, *M. riedeli* Ferguson, 1940, *M. delphax* Marcus, 1946, *M. contortum* Beklemishev, 1951, *M. phytophilum* Beklemishev, 1951, *M. phocorum* Marcus, 1954, *M. spirale* Ax, 1956, *M. poznaniense* Kolasa, 1973, *M. bicurvistyla* Armonies & Hellwig, 1987, and *M. extraculum* Ax & Armonies, 1990. Of these species, however, only *M. leptos*, *M. reynoldsi*, and *M. extraculum* have the characteristic distal enlargement of the stylet which assigns them to the *Macrostromum tuba* group. The other species listed above belong to the *Macrostromum orthostylum* group.

Macrostromum coomerensis, *M. reynoldsi*, *M. extraculum*, and *M. leptos* are differentiated by the different length and outline of their stylets. The stylet of *M. coomerensis* (125 μm in length) is essentially longer than that of both *M. reynoldsi* (72 μm) and *M. extraculum* (68-72 μm). For *M. leptos*, only the length of the body (0.8 mm) and the outline of the stylet are known. The stylet of *M. leptos* differs greatly from that of *M. coomerensis* both in the nature of the distal swelling with subterminal pore and in having the proximal and median part of the stylet greatly

curved. Distally, the stylet is only weakly corkscrew-like.

Macrostomum greenwoodi belongs to the *Macrostomum orthostylum* group based on the curved and evenly tapered distal region of the stylet. The main distinguishing character for this species concerns the outline of the distal termination of the stylet. The distal tip in *M. greenwoodi* is obtuse, with a subterminal ejaculatory duct opening. In this respect, and in not having a cork-screw like stylet, the following 9 species resemble with *M. greenwoodi*: *M. curvituba* Luther, 1947, *M. infundibuliferum* Plotnikov, 1905, *M. johni* Young, 1972, *M. longituba* Papi, 1953, *M. lutheri* Beklemishev, 1927, *M. mediterraneum* Ax, 1956, *M. magnacurvituba* Ax, 1994, *M. mosquense* Beklemishev, 1951, and *M. tenuicauda* Luther, 1947. With the exception of *M. lutheri* and *M. greenwoodi* all other species have stylets with the ejaculatory duct opening subterminally on the concave side of the stylet. The stylets of *M. greenwoodi* and *M. lutheri* have ejaculatory openings subterminally on the convex side of the stylet. *M. lutheri* was established by Beklemishev (1927) only on the characteristic termination of the stylet. Other morphological characters are unknown. Therefore, the only main differential character resides in the complicate enlargement of the distal termination of the stylet.

ACKNOWLEDGEMENTS

Financial support was given by the Deutsche Forschungsgemeinschaft to Dr A. Faubel. We thank Prof. G. Grigg, Head of Zoology

Department, Prof. Jack Greenwood and staff for facilities and help, University of Queensland, Brisbane. Dr L.R.G. Cannon, Queensland Museum, Brisbane and Prof. K. Rohde, University of New England, Armidale, NSW, assisted with help and arrangements.

LITERATURE CITED

- BEKLEMISHEV, V.N. 1927. Über die Fauna des Aralsees. Zugleich ein Beitrag zur Morphology und zur Systematik der Dalyellioidea. Zoologisches Jahrbuch, Systematik 54: 87-138.
- BEKLEMISHEV, V.N. 1951. The species of the genus *Macrostomum* (Turbellaria, Rhabdocoela) of the USSR [in Russian]. Bulletin of the natural Society of Moscow (Biology, new series) 56, 31-40.
- DÖRJES, J. 1968. Die Acoela (Turbellaria) der deutschen Nordseeküste und ein neues System der Ordnung. Zeitschrift für zoologische Systematik und Evolutionsforschung 6: 56-452.
- FAUBEL, A., BLOME, D. & CANNON, L.R.G. 1994. Sandy beach meiofauna of eastern Australia (southern Queensland and New South Wales). I. Introduction and Macrostromida (Platyhelminthes). Invertebrate Taxonomy 8: 989-1007.
- HASWELL, W.A. 1905. Studies on Turbellaria. Quarterly Journal of microscopical Science 49: 425-467.
- TRENCH, R.K. & WINSOR, H. 1987. Symbiosis with dinoflagellates in two pelagic flatworms, *Amphiscolops* sp. and *Haplodiscus* sp. Symbiosis 3: 1-22.
- WINSOR, L. 1988. A new acoel (Convolutidae) from the north Queensland coast, Australia. Fortschritte der Zoologie/Progress in Zoology 36: 391-394.
1990. Marine Turbellaria (Acoela) from north Queensland. Memoirs of the Queensland Museum 28: 785-800.



BOWERBIRD (PTILONORHYNCHIDAE) BIOMETRICS, WITH OBSERVATIONS ON SEXUAL DIMORPHISM AND INTRASPECIFIC VARIATION

CLIFFORD B. FRITH AND DAWN W. FRITH

Frith, C. B. & Frith, D. W. 2001 06 30: Bowerbird (Ptilonorhynchidae) biometrics, with observations on sexual dimorphism and intraspecific variation. *Memoirs of the Queensland Museum* 46(2): 521-542. Brisbane. ISSN0079-8835.

Australasian bowerbirds (Ptilonorhynchidae) belong to 18 or 19 species made up of 35 subspecies. Comprehensive biometrical data are presented for the Ptilonorhynchidae. Mean values and ranges of measurements of each species and subspecies are given, and interspecific and intraspecific variation in size and body proportions discussed. These and plumage traits are used to assess species and subspecies. We accept 20 species including 31 subspecies. *Ailuroedus crassirostris*, *Sericulus ardens* and *Chlamydera guttata* are maintained as species, while *C. nuchalis* subspecies are reduced from four to two. *Ailuroedus melanotis joanae* and *Chlamydera guttata carteri* are considered valid and *Sericulus chrysocephalus rothschildi* invalid. □ Bowerbird, biometrics, sexual dimorphism, variation.

Clifford B. Frith and Dawn W. Frith, 'Prionodura', P.O. Box 581, Malanda 4885, Australia; 8 May 2000.

Gilliard (1969) considered the Australasian bowerbirds (Ptilonorhynchidae) consist of 8 endemic genera, containing 18 species, with 32 subspecies. With subsequent revisions the present consensus has 18 or 19 species, and 35 subspecies (Beehler & Finch, 1985; Christidis & Boles, 1994; Frith et al., 1995; Frith & Frith, 1997a,b, 1999; Schodde & Mason, 1999).

Bowerbirds attract attention particularly because of the elaborate bowers ♂♂ build and decorate. These are related to their polygynous mating system and associated ♂ promiscuity (Gilliard, 1963; Borgia, 1986). Adult ♂♂ show remarkable interspecific diversity of ornate plumages, bower structures and decorations, courtship, and vocalizations. They use these in complex and ritualised displays at traditional sites (Diamond, 1986; Borgia, 1986, 1995; Frith, 1970; Frith & Frith, 1989, 1990, 1993, 1994, 1995a, 2000a,b,c,d; Johnsgard, 1994). Size differences between the sexes (♂♂ typically larger than ♀♀) are particularly pertinent in most polygynous vertebrates but no comprehensive review of size variation among bowerbirds has been published.

Gilliard (1969) provided size ranges for basic traits without indicating either sample sizes or subspecific groupings. Cooper & Forshaw (1977) gave measurements for "five or more specimens" of species. Measurements for some subspecies appear in Schodde & Mason (1999), without sample sizes or means. Biometrical data are available for *Amblyornis* (Schodde & McKean, 1973; Frith & Frith, 1997b, 1998),

Sericulus (Diamond, 1969; Lenz, 1999), *Ptilonorhynchus* (Schodde & Mason, 1999) and *Chlamydera* (Frith & Frith, 1997a, 1999).

Some bowerbird subspecies have been distinguished on geographical plumage and size variation (Gilliard, 1969; Schodde & McKean, 1973; Diamond, 1969, 1972; Coates, 1990; Lenz, 1999; Frith & Frith, 1997a,b; Schodde & Mason, 1999). We examine our biometrical data with respect to subspecies defined by these authors. Differences in average population sizes has limitations, given that size is a continuously varying trait. While this is not a formal taxonomic revision, we record key broad plumage characters where appropriate.

Genera and their sequence herein are a combination of those of Beehler & Finch (1985) and Christidis & Boles (1994). We largely follow Gilliard (1969) at the species and subspecies levels. That is, as taxa are acknowledged in Gilliard's species accounts. Since Gilliard's (1969) text was written *Ailuroedus buccoides oorti* (Mees, 1964), *Se. chrysocephalus rothschildi* (Schodde & Mason, 1999), *C. nuchalis oweni* and *C. n. yorki* (Frith & Frith, 1999) have been rejected. *Al. b. cinnamomeus* (Mees, 1964), *Al. melanotis joanae* (Ford, 1977), *Am. macgregoriae kombok*, *Am. m. nubicola* (Schodde & McKean, 1973), *Am. m. amati* (Pratt, 1982), *Am. m. lecrovayae* (Frith & Frith, 1997b) and *C. guttata carteri* (Frith & Frith, 1997a) have been erected or resurrected. *C. m. guttata* and *Se. aureus ardens* have been raised to species level (Schodde, 1982; Lenz, 1999). We agree with

TABLE 1. Measurements (mm) and weights (g) for *Ailuroedus buccoides*.

	Wing length	Tail length	Tarsus length	Total head length	Bill length	Bill width	Bill depth	Weight
<i>A. b. buccoides</i>								
Males: adult								
Mean	138	90	38.3	63.1	31.4	10.1		172
SD	7.77	5.85	2.31	0.99	2.05	0.71		
Min	123	80	34.1	62.4	27.6	8.5		
Max	149	98	41.6	63.8	33.3	11.1		
n	16	14	14	2	14	13		1
Females: adult								
Mean	130	85	36.9	58.2	29.5	9.5		151
SD	7.14	5.28	1.97	2.24	1.53	0.85		141
Min	116	76	34.6	55.0	27.4	8.3		150
Max	140	94	41.0	61.1	32.2	10.7		152
n	15	15	14	7	15	15		2
<i>A. b. sarak</i>								
Males: adult								
Mean	130	92	38.0	59.7	30.5	9.6		142
SD	3.44	3.13	1.18	1.84	1.46	0.49		5.32
Min	130	86	36.3	57.8	28.0	8.9		135
Max	143	96	40.7	62.6	33.4	10.9		150
n	16	16	16	11	16	16		7
Females: adult								
Mean	132	86	37.2	57.6	28.6	9.1		140
SD	1.91	2.81	1.12	2.14	1.32	0.33		9.05
Min	129	82	35.4	55.8	26.9	8.4		126
Max	135	90	39.1	62.2	31.7	9.5		150
n	12	12	12	7	11	12		7
<i>A. b. cassinianus</i>								
Males: adult								
Mean	134	90	37.7	59.4	30.4	9.7	12.6	139
SD	4.16	3.44	1.57	1.36	1.06	0.60	0.78	12.26
Min	129	84	32.9	56.3	27.6	8.5	12.0	110
Max	143	98	40.6	62.3	32.5	10.7	13.1	159
n	42	35	42	36	42	41	2	23
Females: adult								
Mean	129	85	38.1	57.0	29.1	9.1	11.7	126
SD	4.57	3.30	1.31	1.59	0.91	0.51	0.55	11.82
Min	119	79	33.3	51.9	26.5	8.1	11.1	100
Max	139	93	38.2	60.7	30.9	10.3	12.3	150
n	46	42	45	30	44	44	3	30
<i>A. b. ornithomimus</i>								
Males: adult								
Mean	137	91	39.1	59.1	30.6	10.0		150
SD	4.48	2.79	1.48	1.83	1.33	0.51		
Min	130	85	37.0	56.4	27.1	9.3		
Max	147	95	41.7	62.4	32.6	11.2		
n	19	18	19	11	18	18		1
Females: adult								
Mean	133	87	37.0	57.0	29.2	9.5		130
SD	3.67	2.24	1.19	0.79	1.41	0.52		
Min	129	84	35.4	56.1	27.1	8.7		
Max	141	92	39.3	60.3	31.6	10.5		
n	17	17	16	8	17	16		1
All subspecies								
Males: adult								
Mean	136	91	38.3	59.5	30.6	9.8	12.6	141
SD	5.10	3.75	1.71	1.62	1.29	0.67	0.78	12.27
Min	123	83	32.9	56.3	27.1	8.3	12.0	110
Max	149	99	41.7	63.8	33.9	11.2	13.1	172
n	93	87	91	60	93	86	2	32
Females: adult								
Mean	131	86	36.5	57.3	29.1	9.2	11.7	129
SD	4.91	2.73	1.45	1.88	1.20	0.55	0.55	13.05
Min	118	78	33.3	53.9	26.5	8.1	11.1	100
Max	141	98	41.0	62.2	32.2	10.7	12.3	152
n	90	89	87	52	87	87	5	40

these decisions. *Al. crassirostris* was considered a subspecies of *Al. melanotis* by Schodde & Mason (1999) but see our discussion herein. We

use vernacular names of Bechler & Finch (1985) and Christidis & Boles (1994) except Spotted Catbird for *Al. melanotis* and Yellow-breasted Bowerbird for *C. lauterbachii*; we retain the traditional Black-eared Catbird and Lauterbach's Bowerbird, respectively.

METHODS

We examined all sexed skin specimens with a locality of origin in 32 collections (see Acknowledgements). The catalogue numbers of all specimens used and the measurements taken to produce Tables 1-21 are tabulated and lodged in the library of the Queensland Museum; copies may be obtained from the authors or from the library. Standardized measurements were taken by CBF with the same instruments. 'Wing length' is the flattened and straightened chord, measured with a stopped steel decimal rule. 'Tail centrals' is the maximum length of the longest of the central pair of rectrices, from point of feather entry into skin to its terminal tip, and 'tail length' likewise but to the tip of the longest feather other than the central pair. Tails were measured with an unstopped narrow steel decimal rule. When central and outer tail rectrices were the same length, or <3mm different, only the longer (usually 'tail length') is given. Where there is intrageneric variation, both are given. Other measurements were taken with new fine-pointed steel electronic digital vernier callipers (checked/zeroed daily) to the nearest whole decimal point. 'Bill length' is from the union of bill and fore skull (cranio-maxillary hinge) to the upper mandible tip. We measured bill lengths only from specimens with a complete upper mandible and on which the undamaged cranio-maxillary hinge could be confidently located. 'Bill width' and 'bill depth' (of fully closed bills only) were taken at the anterior nostril edge. 'Total head length' is the maximum distance from rear skull to the upper mandible tip, measured only from specimens retaining sufficient skull bone. Some specimens may appear complete in this respect but are not so total head length figures are minimums. 'Tarsus length' is from the intertarsal joint to the lower edge of the last undivided scute (scale) before the toes diverge. Our measurements of live wild birds were generally similar to those from museum specimens, but we only include live bird measurements where samples of museum specimens are relatively small. Measurements of live birds included are for 10 immature/subadult ♂ *Sc. deminoratus*; 4 adult and 2 immature ♂ and

2 ♀ *Archboldia papuensis sandfordi*; 7 subadult and 42 immature ♂ *Prionodura newtoniana*; 3 adult, 1 subadult and 17 immature ♂ *Pt. violaceus minor*.

As a large majority of Schodde & Mason (1999) wing and tail length ranges fall well within the limits of our ranges we conclude that their samples were smaller. From our samples we evaluate previous assessments of several size-related characters. Gilliard (who used both "culmen" and "culmen from base"), Cooper & Forshaw (1977) and Schodde & Mason (1999) present "culmen length" or "exposed culmen", as opposed to bill length. Culmen length is the same as exposed culmen, and is measured from where anterior forehead feathers no longer cover the culmen to the bill tip, and is not of an entire structure. Thus culmen measurements are shorter, often exclusively, than our bill lengths. Culmen length appears more subjective and variable than bill length and may mislead as it is not structural bill length (Frith & Frith, 1997c: 173; Frith & Beehler, 1998; *Pt. violaceus* below).

Some ♂♂ have a nuchal or fuller crest, which was measured from the posterior crest base to its tip (Schodde & McKean, 1973). We also measured crest length as viewed from above (Frith & Frith, 1997b, 1998). All measurements are in mm. Weights (in grams) were noted from specimen labels. We include additional weights obtained from live birds as follows: 27 adult ♂ and 36 ♀ *Al. m. maculosus*; 46 adult and 10 immature ♂ and 1 ♀ *Sc. dentiostrois*; 3 adult and 2 immature ♂ and 2 ♀ *Ar. p. sanfordi*; 79 adult, 7 subadult, 42 immature ♂ and 12 adult ♀ *Pr. newtoniana*; 3 adult, 1 subadult, and 32 immature ♂ *Pt. v. minor*; 14 adult, 4 subadult ♂♂, and 1 adult ♀ *C. maculata*; 5 adult ♂ *C. nuchalis*. Differences in weight between sexes are commented upon only where samples are adequate, because body weight is subject to bias with respect to time of day/year recorded.

Data are reported for adult samples unless otherwise stated. Data for markedly sexually dimorphic species in which ♂♂ may have an adult, subadult (i.e. trace to almost complete adult ♂ plumage intruding into ♀-type), and immature (purely ♀-type) plumage are presented separately for each age group. For monomorphic species, in which adult ♂♂ and ♀♀ are similar but ♂♂ have a discernibly different immature plumage, data are given separately. Data for ♀♀ are of adults, but some samples might inadvertently include the odd younger

individual, given the similarities of ♀ plumages. We exclude conspicuously smaller individuals (i.e. presumed juveniles-immatures). We do not describe plumages of monotypic species or those of nominate subspecies as these are widely available (Rand & Gilliard, 1967; Gilliard, 1969; Cooper & Forshaw, 1977; Beehler et al., 1986; Coates, 1990; Donaghey, 1996; Schodde & Mason, 1999). In a few instances we refer to numbered colours of Smithe (1975), with his nomenclature indicated by capitalisation. Geographical ranges indicated do not include controversial or vagrant records. West Papua (WP) was Irian Jaya.

SYSTEMATIC NOTES

Family PTILONORHYNCHIDAE

Ailuroedus buccoides (Temminck in Temminck & Laugier, 1835) White-eared Catbird (Tables 1 and 22)

♀♀ average 5% smaller than ♂♂ in tail, tarsus and bill lengths, 6% in bill width, 7% in bill depth and 9% in weight. Tail/wing ratio is 66%, tarsus/wing 28% and bill/wing 22%. Measurements and body size ratios are near uniform across subspecies, except in *geislerorum* which has fractionally shorter wings. We follow Mees (1964) in synonymising *oorti* with *A. b. buccoides*.

Ailuroedus buccoides buccoides (Temminck in Temminck & Laugier, 1835)

Al. b. oorti Rothschild & Hartert, 1913.

♀♀ average 6% smaller in wing, tarsus and bill lengths and bill width than ♂♂. Sexual size dimorphism is little different in the other subspecies. Characterised as "Under surface pale cinnamon with large black dots; crown brown, usually tinged with greenish." (Mees, 1964: 127). Range: W Papuan Islands (Is) and Vogelkop lowlands, coastal W and central Geelvink Bay to Siriwo River (R) in north New Guinea. Triton Bay E to upper Fly R in south New Guinea (NG).

Ailuroedus buccoides stonii Sharpe, 1876

Underparts deep cinnamon, black spots smaller than other subspecies. Crown dark blackish-brown, sometimes tinged greenish, distinctly blacker than in other subspecies. Range: SE coastal Papua New Guinea (PNG) from Amazon Bay to upper Purari R, including

TABLE 2. Measurements (mm) and weights (g) for *Ailuroedus crassirostris*.

	Wing length	Tail length	Tarsus length	Total head length	Bill length	Bill width	Weight
Males: adult							
Mean	166	124	47.1	64.7	34.0	10.0	215
SD	7.35	5.60	1.95	2.50	1.68	0.56	35.41
Min	151	111	40.4	59.6	31.2	8.4	167
Max	179	139	50.0	69.6	38.0	10.8	289
n	38	36	37	25	37	36	13
Females: adult							
Mean	161	120	45.8	63.1	33.2	9.8	193
SD	6.03	5.35	2.16	2.15	1.64	0.51	15.20
Min	150	108	41.6	60.4	30.5	8.9	169
Max	172	127	49.3	67.3	36.9	10.8	211
n	25	25	26	11	26	26	7

the Karimui, Bomai, Soliabeda areas, E Highlands (Diamond, 1972).

Ailuroedus buccoides geislerorum
Meyer, 1892

Al. b. molestus Rothschild & Hartert, 1929.

Underparts as in nominate form but, unlike it and all other subspecies, crown light tan brown. The pure white ear covert feathering extends forward onto the lower lores. Range: Japen Is and north NG from Mamberamo R to Collingwood Bay, PNG.

Ailuroedus buccoides cinnamomeus
Mees, 1964

Underparts save throat deep cinnamon, as in *stonii*, with large black spots. Crown as nominate *buccoides* but on average tinged more green. We found, as did Mees (1964), that at the eastern end of its range 5 of 6 individuals had a darker crown colour, thus approaching *stonii* further east. Range: south WP from Mimika R, E to upper Fly R and Lake Kutubu, PNG.

Al. b. geislerorum is distinctive in its paler tan crown and white ear covert feathering extending forward to include the lower lores. *Stonii* is equally distinctive in its black crown and lores, contrasting pure white ear coverts, and deep cinnamon ventral colouration. *Al. b. buccoides* and *cinnamomeus*, have brown crowns (variably washed greenish). Both have heavy black spotting on the white ear coverts, but *cinnamomeus* has considerably darker cinnamon underparts and usually more white (as opposed to dark brown in *buccoides*) lower lores. These differences are greater than the "northern form, brown cap" and "western and southern form, blackish cap" defined for field use (Beehler et al.,

1986), which may give the erroneous impression of only two subspecies.

***Ailuroedus crassirostris* (Paykull, 1815)**
Green Catbird
(Tables 2 and 22)

♀♀ average 10% lighter than ♂♂. Adult tail/wing length ratio 74%, tarsus/wing length 28% and bill/wing length 20%. Thus this species is proportionately longer-tailed than *Al. m. maculosus* (Table 3), to its N within Australia. Mean bill/tarsus length is 72.3% compared to 77.5% in *Al. m. maculosus*. Range: Coastal Australia from Dawes Range (Ra), Qld to E of Canberra in NSW.

Ailuroedus crassirostris has been considered the southern subspecies of *Al. melanotis* (Pizzey, 1980, 1997; Simpson, 1984, 1999; Schodde, 1976 a,b, 1986) or a separate species (Mack, 1953; Slater, 1974; Slater et al., 1989). Schodde & Mason (1999) argue that "*maculosus* cannot be combined with *melanotis* without bringing in *crassirostris* as well", an argument we do not accept. While the 10 subspecies of *Al. melanotis* demonstrate considerable geographical variation, they all share the traits of a dark crown spotted with conspicuous white to buff markings, strongly contrasting black chin feathering and ear coverts that give a "black-eared" appearance, and broad dusky edging to predominantly whitish throat and chest feathering to give a scalloped appearance. As *Al. crassirostris* (a) lacks the first three characters, (b) has a green throat and chest finely streaked by white central feather lines, (c) is longer tailed and shorter billed than *Al. m. maculosus* and (d) is geographically isolated by more than 600 km, we treat it as a distinct species.

We find the acceptance of *Al. crassirostris* as a species, on morphological and zoogeographical grounds, consistent with similar treatment of *C. guttata* as distinct from *C. maculata* (Christidis & Boles, 1994:74; Schodde & Mason, 1999). The latter are separated by 250 km. *Al. crassirostris* evolved in isolation from *Al. melanotis* stock, the issue being to what level of taxonomic significance it has differentiated. Equivocal (Schodde & Mason, 1999) allele frequency data (Christidis & Schodde, 1992) supported separation of *crassirostris* as a species. Given the foregoing, and that tissue samples remain unavailable for the Aru Is population of *Al. m. melanotis*, for *Al. m. arfakianus*, and for other montane populations (Schodde & Mason, 1999), we concur with Christidis & Boles (1994) in

TABLE 3. Measurements (mm) and weights (g) for *Athroedus melanotis*.

	Wing length	Tail length	Tarsus length	Total head length	Bill length	Bill width	Bill depth	Weight
<i>A. m. melanotis</i>								
Males: adult								
Mean	166	119	45.7	70.0	38.0	11.3		221
SD	6.13	4.14	2.37	2.22	1.68	0.72		21.01
Min	156	112	36.8	66.6	34.9	10.1		200
Max	177	125	48.6	75.4	41.1	12.6		242
n	24	24	25	15	23	23		3
Females: adult								
Mean	158	115	43.6	65.6	35.6	10.6		227
SD	6.95	4.17	1.54	3.13	1.44	0.78		8.524
Min	147	110	40.9	61.4	33.4	9.0		215
Max	166	122	45.7	69.0	37.9	11.4		235
n	10	9	9	4	9	9		4
<i>A. m. maculatus</i>								
Males: adult								
Mean	149	103	43.8	63.2	34.0	9.8	14.1	179
SD	4.38	4.39	1.81	1.57	1.36	0.52	0.77	14.04
Min	140	94	39.9	60.4	29.6	8.7	12.8	145
Max	157	112	47.9	66.0	37.5	11.0	14.7	205
n	57	40	41	23	45	42	5	40
Females: adult								
Mean	146	98	43.1	62.5	33.3	9.3	13.3	169
SD	6.00	4.34	1.82	2.25	1.34	0.55	0.47	14.07
Min	136	90	40.2	57.9	30.9	8.3	12.9	140
Max	159	106	47.0	67.4	35.9	10.7	14.1	199
n	36	30	30	19	30	30	5	50
<i>A. m. artaxianus</i>								
Males: adult								
Mean	162	123	46.7	69.0	37.4	10.8		247
SD	5.11	5.26	1.85	1.85	1.77	0.94		5.77
Min	156	117	44.0	66.5	35.1	9.0		240
Max	171	133	50.3	72.1	40.4	12.0		250
n	11	12	12	8	11	11		3
Females: adult								
Mean	155	119	46.1	65.3	35.5	10.6		216
SD	2.70	2.92	1.06	4.60	1.02	0.62		1.73
Min	151	116	45.2	58.8	34.1	9.7		215
Max	159	123	47.6	68.8	36.6	11.2		218
n	5	5	5	4	5	5		3
<i>A. m. melanocephalus</i>								
Males: adult								
Mean	156	123	46.7	68.2	36.1	10.4		223
SD	4.10	3.35	1.87	2.07	1.47	0.58		29.14
Min	147	116	42.1	63.8	33.6	9.2		204
Max	163	129	51.5	71.5	40.7	11.5		285
n	31	30	31	24	31	31		6
Females: adult								
Mean	150	116	45.2	65.1	34.2	10.0	13.7	203
SD	3.90	3.51	1.49	2.20	1.03	0.53		5.26
Min	143	108	42.4	59.8	31.6	9.3		198
Max	158	121	48.2	68.0	36.1	11.0		210
n	23	23	23	21	23	23	1	4
<i>A. m. jobiensis</i>								
Males: adult								
Mean	162	121	47.5	70.5	39.0	11.4		246
SD	3.32	3.88	2.19	1.59	1.43	0.57		6.42
Min	158	114	43.8	68.8	37.0	10.7		235
Max	166	128	50.1	72.5	41.3	12.5		254
n	12	11	12	7	12	12		6
Females: adult								
Mean	158	119	46.3	65.8	36.2	10.6		233
SD	4.26	3.77	2.26	0.97	1.18	0.41		20.57
Min	152	114	42.8	64.5	34.4	10.2		217
Max	163	125	48.9	66.9	38.2	11.2		261
n	7	7	7	4	7	7		6
<i>A. m. gutturalis</i>								
Males: adult								
Mean	157	115	45.1	69.5	38.6	11.1		225
SD	6.14	2.06	1.39	3.06	1.86	0.79		
Min	149	113	43.1	66.4	34.6	10.3		
Max	162	117	45.1	72.6	38.7	12.0		
n	4	4	4	4	4	4		1
Females: adult								
Mean	153	114	43.6	68.5	36.8	10.9		227
SD	4.72	6.07	1.63	2.10	1.44	0.65		8.524
Min	147	107	41.6	66.4	35.6	10.2		215
Max	158	121	45.6	70.6	39.2	11.8		235
n	5	5	5	3	5	5		4
<i>A. m. ashgimaticus</i>								
Males: adult								
Mean	156	127	47.1	67.0	35.9	10.3		204
SD	5.20	1.64	2.53	1.48	0.73	0.33		10.41
Min	149	124	44.8	65.9	34.6	9.8		196
Max	161	128	51.3	68.0	38.4	10.6		216
n	5	5	5	2	5	5		3
Females: adult								
Mean	153	123	46.1	65.9	34.6	9.7		
SD	0.00	1.41	0.21	0.99	0.07	0.49		
Min	153	122	45.9	65.2	34.5	9.3		
Max	153	124	46.2	66.6	34.6	10.0		
n	2	2	2	2	2	2		
<i>A. m. facialis</i>								
Males: adult								
Mean	160	116	45.9		37.9	10.9		
SD	4.16	1.15	0.56		1.30	0.30		
Min	155	115	45.3		36.6	10.5		
Max	165	117	46.6		39.2	11.2		
n	4	4	4		3	4		
Females: adult								
Mean	157	109	45.0	67.5	35.2	10.6		
SD	4.85	3.18	0.99	1.82	1.02	0.39		
Min	149	104	42.9	64.9	33.6	9.9		
Max	163	113	45.8	68.9	36.7	11.1		
n	7	7	7	4	7	7		
<i>A. m. misolensis</i>								
Males: adult								
Mean	165	140			35			233
SD								
Min								
Max								
n	1	1			1			1
Females: adult								
Mean	169	125.5	45.7	70.7	36.8	11.35		
SD	4.24	0.71	3.18		2.12	1.48		
Min	166	125	43.4		35.3	10.3		
Max	172	126	47.9		38.3	12.4		
n	2	2	2	1	2	2		
<i>A. m. joanae</i>								
Males: adult								
Mean	147	100	42.9	61.9	33.9	9.7		178
SD	2.83	2.12	1.98		2.33	0.07		
Min	145	98	41.5		32.2	9.6		
Max	149	101	44.3		35.5	9.7		
n	2	2	2	1	2	2		1
Females: adult								
Mean	137	94	40.2	59.6	32.2	8.9		150
SD	2.86	4.35	1.04	1.59	0.59	0.29		12.02
Min	133	90	39.1	57.2	31.7	8.4		141
Max	141	100	41.7	61.2	33.2	9.1		158
n	5	4	5	5	5	5		2
All subspecies								
Males: adult								
Mean	156	116	45.6	67.4	36.1	10.5	14.1	198
SD	7.86	9.68	2.35	3.37	2.29	0.86	0.77	30.25
Min	140	94	36.8	60.4	29.6	8.7	12.8	145
Max	177	140	51.5	75.4	41.3	12.6	14.7	285
n	151	133	136	84	137	134	5	66
Females: adult								
Mean	151	110	44.2	64.5	34.4	10.0	13.4	182
SD	7.96	10.08	2.16	3.14	1.68	0.84	0.45	27.37
Min	133	90	39.1	57.2	30.9	8.3	12.9	140
Max	172	126	48.9	70.7	39.2	12.4	14.1	261
n	102	94	95	68	95	95	6	69

maintaining *Al. crassirostris* as a separate species.

***Ailuroedus melanotis* G.R. Gray, 1858**
Black-eared Catbird
(Tables 3 and 22)

Body ratios are similar to those of *Al. crassirostris*. ♀♀ average 5% smaller than ♂♂ in bill width and 8% in weight. Proportions of size sexual dimorphism among the various characters vary slightly between subspecies, but no pattern is evident. Subspecies are generally similar in leg/wing and bill to wing length ratios, but there is some variation in tail/wing length.

Ailuroedus melanotis melanotis
(Gray, 1858).

Darker areas of head plumage and dark edging to the upper breast feathers are blackish to black. Range: Aru Is and Trans-Fly lowlands of south NG.

Ailuroedus melanotis arfakianus
Meyer, 1874

Tail/wing length ratio is 68%. The tail is thus proportionately short, as is that of *joanae* (at 69%). Throat much darker than in *melanotis melanotis*, being black spotted with dirty white to pale buff down to the chest. The latter is not marked blackish as in *melanotis melanotis*, but is darker green marked with narrow and pointed pale buff feather centres. Pale patch behind black ear coverts large and clear white; large spotting on the black crown paler (white or almost so) than in *melanotis melanotis*. Range: Arfak and Tamrau Mountains (Mts), Vogelkop, possibly also Kumawa Mts, WP (Diamond, 1985).

Ailuroedus melanotis maculosus
Ramsay, 1874

Head, nape and upper back less black and far paler than in nominate form, with dark brownish feather edges. Upper back spotting very small, pale buff and feathers lacking blackish edging. Green of back and upper tail paler and slightly more yellowish than in nominate form. Underparts far paler buffy-white, more green, than in *melanotis melanotis* and feathers with broad brown-green edges. Chest far paler and less heavily marked than *melanotis melanotis*. Galbraith (in Mees, 1982) found 4 ♂♂ and 2 ♀♀ had mutually exclusive maxilla depths (11-12.5 versus 10-10.5, respectively) which Mees (1982) thought separated the sexes. In measuring bill depth of 5 of each sex, we found considerable

TABLE 4. Measurements (mm) and weights (g) for *Scenopoeetes dentirostris*.

	Wing length	Tail length	Tarsus length	Total head length	Bill length	Bill width	Bill depth	Weight
Males: adult								
Mean	149	104	31.7	57.6	30.7	10.3	13.5	158
SD	3.86	2.26	1.09	1.77	1.15	0.47	0.43	11.12
Min	141	100	29.4	52.1	28.3	9.4	12.6	132
Max	156	108	34.0	59.8	32.9	11.2	14.4	199
n	35	35	34	23	35	35	20	51
Immature/subadult								
Mean	150	103	31.5	58.7	30.0	10.4	14	164
SD	2.81	1.55	1.81	1.00	1.50	0.31	0.51	12.48
Min	146	101	28.0	57.4	27.2	10.0	13.3	151
Max	155	106	33.0	59.7	31.4	10.7	14.9	185
n	10	8	7	5	7	7	7	10
Females: adult								
Mean	146	101	31.6	58.1	31.0	10.7	13.6	169
SD	3.16	3.08	1.42	1.37	1.16	0.39	0.61	12.62
Min	138	96	29.4	54.0	28.1	9.9	12.7	157
Max	152	107	34.5	59.7	33.0	11.3	14.6	182
n	25	25	25	16	24	26	8	3

overlap. Range: Australian Wet Tropics, from Mt Amos to Seaview-Paluma Ra, Queensland (Qld).

Ailuroedus melanotis melanocephalus
Ramsay, 1883

Tail/wing length ratio is 78%. Like nominate form but underparts generally darker, blacker on chest and throat, and more rufous below. Crown blacker, as the buff spots are slightly smaller and/or sparser (more so in two birds from 'Yule I.'). Range: mountains of SE NG, west to Herzog Mts in north and Mt Karimui in south, including Owen Stanley, Hydrographer, Astrolabe, Wharton and possibly Kratke Mts.

Ailuroedus melanotis jobiensis
Rothschild, 1895

Dorsally like *melanotis melanotis* but spotting on the blackish crown less pure white, more buff. Ventrally quite different in that the chin, throat and upper chest are blackish with only fine buff spotting thereon. Remaining underparts similar to, but darker than *melanotis melanotis*. This subspecies is more like *guttaticollis* ventrally, the throat to upper chest being darker due to smaller pale spotting. White patch behind black ear coverts more obvious than in most subspecies. Range: Bewani, Torricelli, Prince Alexander Mts, middle Idenburg R, and (tentatively) Adelbert Mts, NG.

Ailuroedus melanotis guttaticollis
Stresemann, 1922

Like nominate form but spotting of crown to upper back more rufous, less buffy. Throat and

chin much darker and underparts generally more rufous. In colour and markings indistinct from *jobiensis*. Range: Sepik and (tentatively) Jimi R, PNG.

Ailuroedus melanotis astigmaticus

Mayr, 1931

Tail/wing length ratio is 81%, this being the longest-tailed subspecies. Like *melanotis melanotis* but crown blacker, with fewer, finer, and paler spots. Range: mountains of Huon Peninsula, PNG.

Ailuroedus melanotis facialis Mayr, 1936

Tail/wing length ratio is 71%. Like nominate form but throat darker, less white and more buff. Spotting of crown and upper back much darker, more cinnamon (123A to 123). This is not a "poorly differentiated subspecies" (Cooper & Forshaw, 1977) when compared with its nearest conspecific population of *Al. m. jobiensis*, as the latter has a much darker throat, breast, and crown. Range: Nassau and Oranje Mts, WP.

Ailuroedus melanotis misoliensis

Mayr & de Schaunsee, 1939

Like *arfakianus* but blacker at base of throat, and averaging much larger but with some overlap (Mees, 1965). Range: Misool I, WP.

Ailuroedus melanotis joanae

Mathews, 1941

Tail/wing length is 69%, the tail being similar in length to the other Australian subspecies *maculosus* (68%). Compared to *maculosus*: smaller, blacker on crown, nape, and mantle, less black on face and chin, throat whiter, lower breast, flanks, belly, ventrals and under tail coverts far cleaner (less marked with buff-green feather edging) and thus clean yellowish on these underparts. Differs from other Australian catbirds in having all underwing coverts pure white (save a few exceptions involving only the outermost greater primary coverts). In *Al. crassirostris* and *Al. m. maculosus* these feathers are centrally heavily pigmented with blackish-grey and their edges dirty whitish with the faintest of greenish wash in places. Scalloping on chest notably blacker than on the other Australian subspecies, but less black than on the nominate form in New Guinea to which *joanae* is overall more similar than it is to *maculosus*. Range: QLD, Australia. Pascoe R and Iron Ra areas to Rocky R, McIlwraith Ra, Cape York Peninsula.

Ford (1977) resurrected *joanae* and defined some plumage characters (enlarged upon by Schodde & Mason, 1999) distinctive from *maculosus*. Ironically, the only character Mathews (1941) used in naming *joanae*, that it is smaller than *maculosus*, is invalid. To test this we compared sizes of *joanae* (2 ♂♂ and 5 ♀♀, given that we agree with Ford (1977) that the holotype is ♀) with northernmost *maculosus* from Mt Finnegan (4 ♂♂), Gap Creek, 7 km N of Bloomfield (3 ♂♂, 1 ♀), Granite Creek, Bloomfield R (3 ♂♂, 4 ♀♀), and Big Tableland (2 ♂♂, 1 ♀). Results show *joanae* no smaller than closest *maculosus*.

Scenopoeetes dentirostris (Ramsay, 1876)

Tooth-billed Bowerbird

(Tables 4 and 22)

♀♀ 7% heavier than ♂♂, but this may be due to time of year few weights were taken. This species has by far the shortest proportional tarsus length and is arboreal except when, rarely and briefly, on their forest floor courts (Frith & Frith, 1994). Immature/subadult ♂♂, of Table 4, were all live court-attending birds identifiable as such by their pale mouth (black in adult ♂♂; Frith & Frith, 1995a). Measurements of wing length by Cooper & Forshaw (1977) are near the higher limit of our sample, while most of their other measurements are outside our ranges. As this is the only potentially lekking bowerbird (Frith & Frith, 1995a) in which males form an exploded (vocal rather than visual contact (Johnsgard, 1994)) lek it is surprising to find adult ♂♂ little larger than ♀♀ (and less so than in monogamous *Ailuroedus*). While *Scenopoeetes* has long been considered closest to monogamous *Ailuroedus*, on similarities in plumage and egg colour, behavioural and molecular data indicate its closer relationship to typical, polygynous, genera particularly *Amblyornis* (Frith & Frith, 1993; Kusmierski et al., 1993, 1997; Schodde & Mason, 1999). Range: Australian Wet Tropics uplands, from Mt Amos to Mt Elliot, Qld.

Archboldia papuensis Rand, 1940

Archbold's Bowerbird

(Tables 5 and 22)

♀♀ 8%, 22% and 9% shorter in wing, tail and tarsus lengths, respectively, than ♂♂ but the same in bill length. With a tail/wing length ratio of 96% (103% for ♂♂ only) this is the longest-tailed bowerbird. We assume Gilliard (1969) and Cooper & Forshaw (1977) included some younger individuals in their adult ♂♂

TABLE 5. Measurements (mm) and weights (g) of *Archboldia papuensis*.

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Bill depth	Weight
<i>A. p. papuensis</i>									
Males: subadult									
Mean	159	152	137	39.6	65.2	33.0	8.4		173
SD	2.1	5.7	5.7	0.9	1.5	0.2	0.3		3.5
Min	157	148	133	38.9	64.1	32.8	8.2		170
Max	160	156	141	40.2	66.2	33.1	8.6		175
n	2	2	2	2	2	2	2		2
immature									
Mean	158	135	125	42.2	64.0	32.8	8.2		
SD	3.50	9.68	7.27	1.28	1.01	1.45	0.36		
Min	156	127	120	40.8	62.9	30.7	7.7		
Max	163	148	136	43.9	64.9	34.1	8.5		
n	4	4	4	4	4	4	4		
Females: adult									
Mean	149	126	116	38.1	64.0	33.4	8.9		
SD	4.39	3.65	6.35	1.73	1.42	1.60	0.33		
Min	144	122	112	36.6	62.6	31.0	8.5		
Max	155	130	123	40.7	66.1	35.3	9.2		
n	5	5	3	5	5	5	5		
<i>A. p. sanfordi</i>									
Males: adult									
Mean	168	173	146	43.4	66.3	33.5	8.5	10	184
SD	3.39	8.59	7.29	1.70	1.30	0.91	0.56	0.43	3.88
Min	161	155	133	39.4	64.6	31.8	7.5	8.7	180
Max	174	189	165	45.9	69.8	35.9	9.4	10.3	190
n	21	20	18	21	15	20	20	9	6
immature									
Mean	165	152	137	43.4	66.3	33.6	8.3	9.9	186
SD	1.69	6.72	6.50	1.34	1.03	1.26	0.39	0.38	9.63
Min	163	145	132	41.7	64.4	31.5	7.8	9.6	170
Max	167	162	150	45.4	67.7	35.7	8.8	10.3	195
n	8	7	7	8	7	8	8	3	5
Females: adult									
Mean	158	140	130	40.4	65.3	33.5	8.7	10.0	176
SD	4.74	4.80	4.33	1.65	1.02	1.31	0.70	0.18	9.42
Min	148	132	125	37.1	64.0	31.5	7.8	9.8	163
Max	163	149	139	42.7	66.5	35.6	9.7	10.2	185
n	9	9	8	9	6	9	9	4	4
All subspecies									
Males: adult									
Mean	168	175	148	43.3	66.5	33.6	8.4	9.6	184
SD	3.45	8.25	6.62	1.57	1.32	0.93	0.58	0.16	3.88
Min	161	155	136	39.4	65.0	31.8	7.5	9.4	180
Max	174	189	165	45.5	69.8	35.9	9.4	9.8	190
n	17	16	14	17	11	16	16	5	6
subadult									
Mean	159	152	137	39.6	65.2	33.0	8.4		173
SD	2.1	5.7	5.7	0.9	1.5	0.2	0.3		3.5
Min	157	148	133	38.9	64.1	32.8	8.2		170
Max	160	156	141	40.2	66.2	33.1	8.6		175
n	2	2	2	2	2	2	2		2
immature									
Mean	163	146	133	43.0	65.6	33.4	8.3	9.9	186
SD	4.23	11.59	8.89	1.39	1.48	1.33	0.36	0.36	9.63
Min	156	127	120	40.8	62.9	30.7	7.7	9.6	170
Max	167	162	150	45.4	67.7	35.7	8.8	10.3	195
n	12	11	11	12	10	12	12	3	5
Females: adult									
Mean	154	135	126	39.5	64.7	33.5	8.8	10.0	176
SD	6.70	6.37	6.10	1.97	1.32	1.36	0.58	0.18	9.42
Min	144	122	112	36.6	62.6	31.0	7.8	9.8	163
Max	163	149	139	42.7	66.5	35.6	9.7	10.2	185
n	14	14	11	14	11	14	14	4	4

because their wing length ranges of 155-170 and 155-162 are small versus our 161-174. The two geographically isolated forms of this bird are considered separate species by some (Gilliard, 1951, 1958, 1959; Peckover & Filewood, 1976; Collar, 1986) and indistinct, or invalid, subspecies by others (Frith et al., 1995). While lack of adult ♂ specimens of *papuensis*

TABLE 6. Measurements (mm) and weights (g) of *Amblyornis inornatus*.

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
Males: adult								
Mean	134	95	93	36.4	60.7	30.1	8.4	128
SD	3.37	3.77	3.84	1.37	1.70	1.43	0.51	15.51
Min	129	88	84	34.0	57.2	27.4	7.3	105
Max	140	104	100	39.2	63.8	33.1	9.7	155
n	28	28	26	28	19	27	27	12
Females: adult								
Mean	130	91	91	35.2	60.2	30.2	8.6	121
SD	3.11	2.77	3.00	1.18	1.89	1.37	0.87	15.21
Min	125	85	84	33.4	57.8	27.9	6.9	105
Max	136	96	95	37.8	63.7	32.1	10.0	146
n	18	18	17	18	14	18	18	9

papuensis hampers comparisons, adult ♀♀ (Table 5) are smaller than those of *sanfordi*.

Archboldia papuensis papuensis Rand, 1940

The smaller subspecies, averaging 6% smaller in wing and tarsus length, and 10% in tail length (♀♀ only), but similar in bill size. This difference in tail length is exclusive, the range in this form being 122-130 but in *sanfordi* 132-149. The adult tail/wing length ratio averages 96% in ♂♂ and 85% in ♀♀. Plumage is generally less black, more grey, than that of *sanfordi*. Range: Ibele R (Balim Valley) to Lake Habbema region, Oranje Mts, Nassau Ra and Wissel Lakes, Weyland Mts area, WP.

Archboldia papuensis sanfordi Mayr & Gilliard, 1950

Larger than *papuensis papuensis* and plumages blacker. Tail/wing length ratio averages 103% in ♂♂ and 89% in ♀♀. Adult ♂♂ fully crested. Mean exposed crest length of 20 ♂♂ is 91 (77-98, SD 5.41). Range: Mt Hagen, Giluwe, Tari Gap and S Karius Ra (unconfirmed on Kubor Ra), PNG (Coates, 1990).

Amblyornis inornatus (von Rosenberg in Schlegel, 1873) Vogelkop Bowerbird (Tables 6 and 22)

♀♀ average fractionally smaller than ♂♂ in body sizes and weight. Both sexes in this and other *Amblyornis* are identical or similar in tail/wing length ratios (Table 21), a trait shared by *Scenopoeetes* among polygynous genera (and also by monogamous *Ailuroedus*). Range: Arfak, Tamrau, Wandammen, Kumawa, and Fakfak Mts, WP (Diamond, 1987; Uy & Borgia, 2000).

TABLE 7. Measurements (mm) and weights (g) of *Amblyornis macgregoriae*.

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Bill depth	Weight
<i>A. m. macgregoriae</i>									
Males: adult									
Mean	135	87	85	37.4	57.9	28.0	7.6		120
SD	3.22	3.35	3.19	1.04	0.95	0.63	0.65		13.47
Min	129	81	79	35.5	55.4	26.8	6.7		104
Max	142	92	91	40.0	59.3	30.1	8.9		142
n	22	22	20	22	13	22	22		7
immature									
Mean	133	87	86	37.3	57.3	27.5	7.4		120
SD	3.84	3.55	3.49	1.43	1.16	1.23	0.48		8.22
Min	126	80	80	34.6	55.6	25.2	6.5		110
Max	139	92	91	40.6	60.1	29.9	8.2		139
n	22	21	19	22	16	22	22		14
Females: adult									
Mean	131	85	83.4	36.1	58.2	28.5	8.0	8.9	123
SD	3.42	3.12	3.02	1.10	1.54	0.82	0.50		5.71
Min	123	78	77	33.3	54.1	27.0	6.8		115
Max	138	90	90	38.0	59.9	29.6	9.3		130
n	26	26	22	26	19	26	25		7
<i>A. m. permanentis</i>									
Males: adult									
Mean	130	87	84	36.3	57.8	27.1	7.3	9.6	112
SD	3.11	1.92	2.19	0.88	1.46	0.66	0.38		8.68
Min	124	85	81	34.9	56.0	26.0	6.6		104
Max	135	90	86	37.8	59.7	28.5	7.9		127
n	11	11	9	11	6	11	11	1	5
immature									
Mean	126	86	84	36.6	55.9	26.7	7.7		114
SD	2.56	2.26	3.33	0.64	1.36	1.18	0.31		2.87
Min	122	83	78	35.3	53.4	24.6	7.3		112
Max	130	89	87	37.8	57.0	28.3	8.2		118
n	8	8	6	8	6	8	7		4
Females: adult									
Mean	127	86	84	36.0	57.3	26.5	8.3		115
SD	1.57	3.51	3.99	0.78	1.88	0.85	0.65		7.68
Min	125	81	78	35.2	55.1	27.5	7.2		108
Max	129	92	91	37.3	58.5	29.6	9.2		125
n	7	7	7	7	3	7	7		4
<i>A. m. mayi</i>									
Males: adult									
Mean	139	92	89.5	37.7	59.8	29.3	8.2	9.5	143
SD	2.99	3.06	2.87	1.86	2.10	0.69	0.64		3.54
Min	134	87	83	33.8	55.4	28.4	7.0		140
Max	145	98	95	40.3	62.4	30.6	9.4		145
n	22	21	20	22	10	21	21	1	2
immature									
Mean	138	89	87.6	37.6	58.4	28.9	7.9		127
SD	3.37	4.70	5.60	1.00	1.76	1.10	0.60		6.43
Min	131	81	78	35.3	56.7	27.4	6.8		120
Max	143	99	99	38.9	60.7	31.6	8.8		132
n	15	14	13	15	7	15	15		3
Females: adult									
Mean	134	89	86.6	36.4	59.1	30.2	8.6		
SD	3.16	3.83	3.56	0.81	2.11	1.97	0.61		
Min	127	83	80	34.4	54.9	27.3	7.0		
Max	142	98	94	38.1	62.4	30.6	9.6		
n	26	26	25	26	13	26	26		
<i>A. m. kombok</i>									
Males: adult									
Mean	137	87	84	37.4	58.1	28.1	7.4	9.0	125
SD	3.68	3.20	3.69	1.91	1.67	0.90	0.59	0.58	9.27
Min	129	79	73	27.9	55.4	26.5	6.2	8.5	110
Max	144	92	90	40.0	60.7	30.1	8.3	9.5	140
n	37	32	27	36	17	37	35	5	7
immature									
Mean	135	85	83	37.8	57.9	27.8	7.5	9.0	121
SD	3.66	2.60	2.64	0.97	1.26	0.79	0.60	0.21	9.35
Min	128	80	80	36.2	56.1	26.3	6.7	8.0	110
Max	141	90	88	39.2	59.9	29.6	8.7	9.7	134
n	17	17	17	17	10	17	17	2	7
Females: adult									
Mean	131	84	81	36.1	57.4	28.0	8.3	9.2	130
SD	3.13	2.92	2.91	1.94	2.31	0.80	0.74	0.48	14.14
Min	127	78	77	30.7	50.0	27.6	7.0	8.5	120
Max	138	88	87	39.8	59.7	30.2	9.6	10.1	140
n	19	18	11	19	15	19	19	7	2

<i>A. m. rubicula</i>									
Males: adult									
Mean	135	91	80	37.1	58.2	27.8	6.7		128
SD	1.73	3.14	3.88	0.90	0.71	0.95	0.25		5.69
Min	133	89	87	36.2	57.6	26.8	6.4		122
Max	138	95	94	38.0	59.0	28.7	6.9		133
n	3	3	3	3	3	3	3		3
immature									
Mean	134	91	89	36.3	56.7	28.1	7.3		128
SD	1.72	2.51	2.07	1.30	1.55	0.92	0.30		3.95
Min	132	87	85	34.6	56.0	26.8	7.0		125
Max	137	95	92	36.1	60.5	29.5	7.8		135
n	7	7	7	7	7	7	7		7
Females: adult									
Mean	131	89	88	35.5	57.9	28.1	7.6		130
SD	2.65	2.99	2.52	1.21	0.62	0.40	0.26		7.33
Min	128	86	85	33.7	57.0	27.5	7.3		119
Max	137	95	92	38.1	60.5	29.5	7.8		135
n	3	4	3	4	4	4	3		4
<i>A. m. amabilis</i>									
Males: adult									
Mean	128	82	80.1	35.7		26.2	7.2		
SD	1.41	0.35		1.84					
Min	127	82		34.4					
Max	129	82.5		37.0					
n	2	2	1	2		1	1		
<i>A. m. leucophaea</i>									
Males: adult									
Mean	132	82	80	36.8	54.4	27.9	8.0	9.3	
SD	1.67	2.58	3.56	0.95	1.34	1.16	0.57		
Min	130	78	75	35.3	53.4	26.9	7.5		
Max	135	84	84	37.7	55.3	29.7	8.8		
n	6	5	5	5	2	5	5	1	
immature									
Mean	131	82	81	36.5		27.6	7.4		
SD	2.00	1.20	2.25	3.46		0.59	0.42		
Min	129	80	79	34.0		27.2	7.1		
Max	133	83	83	38.9		28.3	7.9		
n	3	3	3	2		3	3		
Females: adult									
Mean	129	81	81	37.9		26.6	8.1		
n	1	1	1	1		1	1		
All subspecies									
Males: adult									
Mean	136	88	86	37.2	58.2	28.2	7.6	9.2	123
SD	4.36	4.02	4.16	1.62	1.83	1.07	0.67	0.39	12.33
Min	124	78	73	27.9	53.4	25.9	6.2	8.5	104
Max	145	98	95	40.3	62.4	30.8	9.4	9.6	145
n	102	96	85	101	51	100	98	8	24
immature									
Mean	133	87	85	37.3	57.6	27.8	7.5	9.0	122
SD	4.38	3.97	4.16	1.29	1.56	1.22	0.54	0.21	8.10
Min	122	80	78	34.0	53.4	24.6	6.5	8.8	110
Max	143	99	98	40.6	60.7	31.6	8.8	9.1	139
n	72	70	65	71	46	72	71	2	35
Females: adult									
Mean	132	86	84	36.2	58.1	29.1	8.3	9.2	124
SD	3.64	4.04	3.77	1.27	1.96	1.48	0.65	0.46	8.97
Min	123	78	77	30.7	50.0	26.8	6.8	8.8	108
Max	142	98	94	39.8	62.4	30.6	9.6	10.1	140
n	82	82	89	83	54	83	81	8	17

***Amblyornis macgregoriae* De Vis, 1890**
Macgregor's Bowerbird
 (Tables 7 and 22)

♀♀ average 9% wider in bill width than ♂♂, both sexes having all but the same bill length. Mean crest length from posterior base of 47 ♂♂ is 64 (46-75, SD 6.56) and exposed crest length of 96 ♂♂, 82 (52-105, SD 10.26).

Amblyornis macgregoriae macgregoriae
De Vis, 1890

Most similar in size to *kombok* and in proportions, for both sexes, to *rubicola* and *kombok* ♀♀ average 5% wider in bill width than

TABLE 8. Measurements (mm) and weights (g) of *Amblyornis subalaris*.

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
Males: adult								
Mean	125	89	65	34.6	56.4	25.9	7.3	96
SD	2.60	2.97	3.25	1.57	1.44	1.26	0.37	
Min	121	80	77	30.1	54.6	23.5	6.7	
Max	130	94	92	36.7	60.0	28.5	8.0	
n	30	28	27	29	22	23	29	1
subadult								
Mean	123	87	86	34.2	56.5	25.4	7.1	96
SD	1.00	1.15	1.13	1.41	0.42	0.31	0.56	
Min	122	66	65	32.9	56.2	25.1	6.6	
Max	124	88	87	35.7	56.6	25.7	7.6	
n	3	3	3	3	2	3	3	1
immature								
Mean	124	89	86	34.7	55.5	25.9	7.5	109
SD	2.30	2.95	3.39	0.76	1.93	1.00	0.52	8.38
Min	121	84	82	33.5	52.8	24.4	6.6	104
Max	128	93	92	35.9	58.5	27.6	8.5	126
n	11	10	10	11	8	11	11	6
Females: adult								
Mean	124	87	85	34.1	56.0	26.5	7.8	108
SD	3.14	2.74	2.36	1.57	1.15	1.18	0.48	9.66
Min	117	81	80	30.7	55.2	24.8	6.7	95
Max	131	92	88	38.4	59.5	29.6	8.5	122
n	22	22	22	22	17	21	21	5

♂♂. Mean crest length from posterior base of 1 ♂ 65 and exposed crest length of 22 ♂♂ 81 (55-92, SD 9.50). Range: W Kukukuku and Herzog Ra to W Owen Stanley Ra, PNG, excluding range of *Am. m. nubicola* to the E (Schodde & McKean, 1973).

Amblyornis macgregoriae germanus
Rothschild, 1910

Both sexes average 7% lighter and fractionally smaller in wing length than *macgregoriae macgregoriae*, but almost identical to it in tail length and similar in tarsus and bill lengths and bill width. Mean crest length from posterior base of 3 ♂♂ 48 (46-50, SD 2.08) and exposed crest length of 10 ♂♂ 68 (56-79, SD 6.51). Range: mountains of Huon Peninsula, PNG.

Amblyornis macgregoriae mayri
Harteri, 1930

The largest subspecies, ♀♀ 5% wider in bill width than ♂♂. Mean crest length from posterior base of 2 ♂♂ 72 (71-73, SD 1.63) and exposed crest length of 22 ♂♂ 90 (79-105, SD 7.79). Range: Weyland Mts, WP to E Star/W Hindenburg Mts, extreme western PNG.

Amblyornis macgregoriae kombok
Schodde & McKean, 1973

Similar in size and proportions to the nominate form. In bill width, ♀♀ average 12% larger than

♂♂. Mean crest length from posterior base of 28 ♂♂ 63 (51-71, SD 4.92) and exposed crest length of 32 ♂♂ 84 (72-93, SD 5.59). Crest rather dense. Throat and upper breast pale-brownish olive; lower breast, abdomen, and under tail-coverts rather bright light buffy brown (Schodde & McKean, 1973). Range: Kubor, Hagen and Bismarck Ra, central PNG, probably W to at least the Strickland R or Hindenberg Ra, and E to Kratke Ra (Schodde & McKean, 1973).

Amblyornis macgregoriae nubicola
Schodde & McKean, 1973

The tail/wing length ratio fractionally longer than average for the species (as in *germanus*). In bill width, ♀♀ average 13% wider than ♂♂. Mean exposed crest length of 3 ♂♂ 83 (75-90, SD 7.75). ♂ crest length from posterior base 59-65 (n=3, SD=3.0) and rather densely feathered, entire under surface uniformly dull coffee-brown. Range: Mt Simpson-Dayman area, E Owen Stanley Ra, probably W to Mt Suckling, PNG (Schodde & McKean, 1973).

Amblyornis macgregoriae amati
Pratt, 1982

2 ♂ specimens indicate this is the smallest subspecies, with wing length closest to *germanus* and tail as in *leeroyae*. Mean crest length from posterior base of 1 ♂ 71 and exposed crest length of 2 ♂♂ 54 (52-57, SD 3.18). Chin, throat and upper breast dark olive brown, only slightly paler than side of head and forehead; breast medium coffee brown. Range: Adelbert Mts, PNG.

Amblyornis macgregoriae leeroyae
Frith & Frith, 1997

A small and particularly short-tailed form, similar to *amati* in size. Tail/wing length averages fractionally shorter than for the species. Of 5 ♂♂, mean crest length from posterior base 64 (62-66, SD 1.64) and exposed crest length 76 (67-83, SD 6.64). Darker and more brown-orange than *kombok*. Range: NNW slopes of Mt Bosavi, PNG.

Amblyornis subalaris Sharpe, 1884
Streaked Bowerbird
(Tables 8 and 22)

Smallest, and relatively shortest winged, *Amblyornis* species. ♀♀ average fractionally smaller than ♂♂. Mean crest length from posterior base of 1 ♂ 50; the exposed crest length of 29 ♂♂ 61 (50-72, SD 5.79), and that of a crested ♀ 30. The species is known to have

TABLE 9. Measurements (mm) and weights (g) of *Amblyornis flavifrons*.

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width
Males: adult							
Mean	137	85	82	34.2	58.4	30.8	7.9
SD	2.65	1.15	3.46	0.85	1.41	5.78	0.64
Min	135	84	80	33.4	57.4	27.2	7.5
Max	140	86	86	35.1	59.4	37.5	8.6
n	3	3	3	3	2	3	3

hybridised at least once with *Am. macgregoriae*. Range: Mountains of extreme SE of NG, from upper Angabunga R to Mts Suckling, Simpson and Moiba, PNG (Schodde & McKean, 1973).

***Amblyornis flavifrons* Rothschild, 1895**
Golden-fronted Bowerbird
(Tables 9 and 22)

♂ wing length similar to *Am. macgregoriae*. Short-tailed relative to wing length, and long-winged relative to tarsus length, compared with *Am. macgregoriae*. Mean crest length from posterior base of 2 ♂♂ 54 (53-54, SD 0.71) and exposed crest length of 3 ♂♂ 94 (89-97, SD 4.16). No ♀ collected. Range: Foya (or Gauttier) Mts of WP (Diamond, 1982).

***Prionodura newtoniana* De Vis, 1883**
Golden Bowerbird
(Tables 10 and 22)

Immature (♀-plumaged) ♂♂ all-but identical in body measurements to adult ♀♀ but, like adult ♂♂, average slightly smaller in tarsus and bill lengths and notably more so in bill width and depth. The great disparity between ♂ and ♀ tail length, and the relative proportions of these, reflects sexual selection upon ♂♂ for arboreal/flight courtship display traits (Frith & Frith, 2000b,d). Other than this, ♀♀ are fractionally larger, averaging 15% heavier, than ♂♂ but influences of sampling bias upon the latter are unknown. Range: Australian Wet Tropics uplands, from Thornton Ra and Mt Windsor Tableland to Seaview-Paluma Ra, Qld (Nix & Switzer, 1991).

***Sericulus aureus* (Linnaeus, 1758)**
Masked Bowerbird
(Tables 11 and 22)

Both sexes average almost the same wing length. ♀♀ average 5% and 7% larger in tail length and bill width but 7% and 6% smaller in

TABLE 10. Measurements (mm) and weights (g) of *Prionodura newtoniana*.

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Bill depth	Weight
Males: adult									
Mean	122	110	95	30.3	50.9	23.1	6.0	7.0	73
SD	1.53	3.50	2.24	1.20	0.74	0.54	0.29	0.16	5.13
Min	119	88	85	23.1	49.0	22.0	5.4	6.7	62
Max	126	115	98	32.3	52.4	24.4	7.0	7.4	86
n	74	60	57	57	41	49	55	47	80
subadult									
Mean	119	87	84	29.9	50.7	23.3	6.6	6.9	71
SD	1.28	3.72	1.51	0.89	0.30	1.01	0.46	0.62	2.67
Min	118	79	82	29.0	50.3	21.7	6.2	5.9	68
Max	122	91	86	31.3	51.1	24.3	7.0	7.4	76
n	8	8	7	5	5	5	4	5	7
immature									
Mean	119	88	85.1	30.9	50.0	23.1	6.4	7.18	75
SD	1.76	2.17	2.10	0.67	0.82	0.66	0.40	0.26	3.77
Min	115	84	78	29.2	48.8	21.3	5.4	6.4	69
Max	124	99	90	32.1	51.5	24.2	7.4	8.1	82
n	56	55	52	41	14	42	43	33	42
Females: adult									
Mean	119	88	85	30.8	50.9	23.7	6.8	7.5	84
SD	2.54	1.91	1.94	0.79	2.11	0.70	0.52	0.22	8.36
Min	112	85	80	28.7	47.4	22.3	5.6	7.1	62
Max	124	92	88	32.3	56.4	25.1	7.8	7.8	96
n	30	30	27	28	15	30	29	11	17

bill depth and weight than ♂♂, respectively. With tail/wing length ratio of 60%, this bowerbird has the third shortest proportionate tail. Gilliard's culmen "from base" should be compatible with our bill length, but his 23 for ♂♂ and 24 for ♀♀ are shorter and therefore probably of exposed culmen. Moreover, his ♀ wing length of 137-140 is 2mm shorter than our shortest. Range: Mountains of western and northern NG almost to the Sepik R in the E.

TABLE 11. Measurements (mm) and weights (g) of *Sericulus aureus*.

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Bill depth	Weight
Males: adult	143	84	82	41.4	61.2	30.6	7.5	8.5	178
Mean	3.37	3.72	3.55	1.23	1.98	1.61	0.34	0.26	3.54
SD	136	77	78	39.7	57.4	25.9	6.8	7.9	175
Min	151	90	88	44.1	64.8	32.6	8.3	8.8	180
Max	22	21	15	18	18	22	11	11	2
n									
subadult									
Mean	147	87	86	42.3	62.9	31.5	7.5	8.6	171
SD	2.86	2.95	3.40	1.44	1.22	1.25	0.52	0.30	7.78
Min	142	81	81	40.3	59.8	29.5	6.6	8.2	165
Max	151	91	92	44.8	64.4	33.1	8.2	8.9	176
n	11	11	9	11	11	11	11	4	2
immature									
Mean	139	90	89	42.0	60.8	32.0	7.5		149
SD	2.63	5.19	8.08	0.73	2.65	1.79	0.68		9.91
Min	135	83	80	41.0	57.3	30.2	6.7		135
Max	141	94	94	42.6	64.2	34.2	8.3		156
n	4	4	3	4	6	4	4		4
Females: adult									
Mean	142	88	87	41.9	61.8	31.5	8.0	7.9	168
SD	2.07	4.81	6.04	1.41	1.00	1.09	0.68	0.14	5.77
Min	139	82	79	40.1	60.4	29.8	6.8	7.8	165
Max	146	97	97	44.7	63.3	33.3	8.9	8.0	175
n	11	10	7	11	10	10	11	2	3

TABLE 12. Measurements (mm) and weights (g) of *Sericulus ardens*.

	Wing length	Tail length	Tail centrale	Tarsus length	Total head length	Bill length	Bill width	
Males: adult								
Mean	138	65	64	42.2	60.7	29.6	7.4	
SD	4.12	3.02	3.33	2.64	1.28	0.47	0.49	
Min	135	62	60	36.0	58.7	28.8	6.5	
Max	148	72	70	44.6	62.0	30.3	8.1	
n	9	9	8	9	6	8	8	
subadult								
Mean	141	70	67	42.6	59.1	29.0	7.4	
SD	2.99	3.10	3.79	1.72	0.70	0.40	0.58	
Min	138	67	63	40.1	58.4	28.4	6.9	
Max	145	74	70	43.7	59.8	29.3	8.2	
n	4	4	3	4	3	4	4	
Females: adult								
Mean	143	74	73	41.8	59.9	28.9	7.8	
SD	4.95	1.41	2.12	0.07	0.14	0.57	0.07	
Min	139	73	71	41.7	59.8	28.5	7.7	
Max	146	75	74	41.8	60.0	29.3	7.8	
n	2	2	2	2	2	2	2	

Sericulus ardens
(D'Albertis & Salvadori, 1879)
Flame Bowerbird
(Tables 12 and 22)

Sericulus aureus has a tail longer than *Se. ardens* and averages a slightly longer (and pale) bill. This results in strikingly different tail/wing length ratios of 60% and 50%, respectively, the

TABLE 13. Measurements (mm) and weights (g) of *Sericulus bakeri*.

	Wing length	Tail length	Tail centrale	Tarsus length	Total head length	Bill length	Bill width	Weight
Male: adult								
Mean	138	79	76	41.8	60.1	30.0	8.0	182
SD	1.30	2.35	2.65	0.63	1.02	0.58	0.39	2.12
Min	136	77	73	41.1	58.3	29.0	7.6	180
Max	139	83	80	42.8	60.7	30.4	8.5	183
n	5	5	5	5	5	5	5	2
subadult								
Mean	143	85	83	42.5	60.8	30.6	8.5	178
SD	0.71	2.12	1.41	1.48	0.07	0.21	0.14	
Min	142	83	82	41.4	60.7	30.4	8.4	
Max	143	86	84	43.5	60.8	30.7	8.6	
n	2	2	2	2	2	2	2	1
immature								
Mean	139	83	82	41.8	59.5	29.7	7.7	170
SD	4.95	5.66	7.07	0.49	0.07	0.78	0.49	
Min	135	79	77	41.4	59.4	29.1	7.3	
Max	143	87	87	43.5	60.8	30.7	8.6	
n	2	2	2	2	2	2	2	1
Females: adult								
Mean	139	85	84	40.5	60.6	31.5	8.6	173
SD	3.10	4.13	3.85	1.99	1.47	0.76	0.48	8.38
Min	133	80	80	38.7	58.3	30.6	7.9	164
Max	142	91	91	43.2	62.4	32.9	9.2	184
n	6	6	6	6	5	6	6	5

TABLE 14. Measurements (mm) and weights (g) of *Sericulus chrysocephalus*.

	Wing length	Tail length	Tail centrale	Tarsus length	Total head length	Bill length	Bill width	Bill depth	Weight
Males: adult									
Mean	130	85	79	34.9	58.5	30.9	5.9	6.9	90
SD	2.56	2.19	2.82	1.26	0.90	0.73	0.30	0.28	12.44
Min	125	82	74	32.5	56.6	29.3	5.5	6.4	76
Max	135	91	86	36.8	60.1	32.3	6.5	7.3	110
n	23	23	22	21	37	21	21	12	5
subadult									
Mean	134	92	85	34.6	56.4	30.6	5.9	7.2	86
SD	2.28	4.65	8.02	1.16	1.95	0.54	0.22	0.26	
Min	131	87	77	33.4	53.6	30.0	5.6	6.9	
Max	137	98	96	36.5	58.0	31.3	6.2	7.4	
n	5	4	4	5	4	4	5	3	1
immature									
Mean	133	99	95	34.6	57.3	30.0	6.1	6.9	90
SD	2.88	2.58	3.10	1.02	1.08	0.87	0.24	0.39	3.90
Min	129	94	91	32.9	55.7	28.8	5.9	6.3	85
Max	140	105	102	36.2	59.0	31.1	6.8	8.0	97
n	14	14	14	14	14	14	14	14	13
Females: adult									
Mean	138	106	102	35.6	57.8	30.4	7.0	7.7	111
SD	3.85	3.36	3.29	1.03	1.13	0.96	0.37	0.29	12.13
Min	131	96	93	34.0	55.7	27.9	6.0	7.1	95
Max	148	111	107	38.2	59.7	32.1	7.5	8.2	134
n	26	26	21	26	26	26	26	23	20

latter having a shorter tail than other bowerbirds (Table 21). Sexual size dimorphism is also quite different in the two species: ♀ *ardens* average 14% and 5% larger in tail length and bill width but fractionally smaller in tarsus and bill lengths than ♂♂. Our bill width figures do not agree well with Lenz's (1999: 53) statement that *ardens* has a "much narrower bill than *aureus*". The bill width figures of Lenz (1999, table 3.8) do not support his statement. They do, however, indicate ♂ *ardens* have a slightly narrower bill than ♂ *aureus* and that *aureus* has a deeper bill than *ardens*. In size differences between the sexes, and in body proportion ratios of the 3 *Sericulus* species in New Guinea, *aureus* differs more from *ardens* than it does from *bakeri*. Range: Patchy in lowlands-foothills from Wataikwa-Mimika, upper Noord-Endrich R of WP to upper Fly R, Strickland-Nomad R and Mt Bosavi, PNG (Mackay, 1984).

Se. a. aureus and *Se. a. ardens* have different ♂ plumages and bill colouration (Cooper & Forshaw, 1977; Beehler et al., 1986). They are all but allopatric, in being isolated by the central ranges, and are restricted to predominantly different altitudes, but do meet and hybridise on the Wataikwa R, south WP as indicated by 1 or 2 ♂♂ specimens (Gilliard, 1969). Thus, *aureus* and *ardens* are considered separate species (Lenz, 1999).

TABLE 15. Measurements (mm) and weights (g) of *Ptilonorhynchus violaceus*.

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
<i>P. v. violaceus</i>								
Males: adult								
Mean	172	110	103	49.3	66.5	35.4	9.8	238
SD	3.88	5.20	5.45	1.98	1.38	1.70	0.34	19.5
Min	162	103	95	44.3	63.7	31.5	9.0	208
Max	182	125	114	53.0	69.4	40.3	10.4	278
n	66	46	27	47	30	46	46	13
subadult								
Mean	173	115	115	48.3	66.5	35.7	9.7	205
SD	3.77	4.92		2.37	1.51	0.67	0.46	
Min	168	109		45.3	64.8	35.3	9.4	
Max	177	121		50.2	67.7	36.5	10.2	
n	4	4	1	4	3	3	3	1
intermediate plumaged immature								
Mean	171	119	114	49.3	66.1	34.9	10.1	227
SD	3.98	5.34	4.35	2.38	1.52	1.06	0.29	25.97
Min	161	106	107	43.7	61.7	32.6	9.5	176
Max	178	131	125	53.7	67.7	37.5	10.6	284
n	26	26	18	26	17	26	26	14
female-plumaged immature								
Mean	169	118	111	49.8	65.3	34.3	9.9	225
SD	3.90	4.55	5.50	1.84	1.53	1.08	0.34	8.79
Min	162	107	103	46.7	62.0	32.5	9.2	208
Max	178	126	120	54.2	67.8	35.9	10.4	234
n	21	20	14	21	18	21	21	12
Females: adult								
Mean	165	117	113	46.1	64.1	34.6	10.2	209
SD	4.74	4.67	4.72	2.15	1.50	1.50	0.33	18.80
Min	156	108	102	41.5	60.1	31.0	9.6	170
Max	176	128	123	51.6	67.2	38.2	10.9	250
n	60	59	36	60	43	59	58	30
<i>P. v. minor</i>								
Males: adult								
Mean	153	96	89	47.3	63.9	33.2	9.3	187
SD	2.74	2.80	2.34	1.84	1.20	0.86	0.81	16.70
Min	150	92	87	44.3	62.0	32.0	8.4	173
Max	158	100	93	49.6	65.1	34.4	11.3	205
n	10	10	7	10	7	9	10	4
subadult								
Mean	156	102	97	47.9	64.5	33.4	9.8	206
n	1	1	1	1	1	1	1	1
intermediate-plumaged immature								
Mean	153	101	97	45.9	62.4	32.3	9.8	193
SD	4.85	3.21	3.25	2.35	1.29	0.78	0.37	23.08
Min	144	93	90	41.4	60.5	30.9	9.0	164
Max	165	110	104	48.9	64.2	33.4	10.3	232
n	18	18	17	18	17	18	18	18
female-plumaged immature								
Mean	152	102	98	47.4	62.3	33.3	8.8	197.8
SD	4.73	3.79	2.31	1.18		0.75	0.81	15.20
Min	148	99	95	46.7		32.6	7.9	187
Max	157	106	99	48.8		34.1	9.5	209
n	3	3	3	3	1	3	3	2
Females: adult								
Mean	150	102	95	45.0	61.5	31.7	9.5	174
SD	4.65	3.32	3.30	1.67	0.21	0.50	0.32	
Min	145	98	91	43.6	61.3	31.3	9.2	
Max	156	106	99	47.0	61.7	32.4	9.9	
n	4	4	4	4	3	4	4	1
All subspecies								
Males: adult								
Mean	169	108	100	48.9	66.1	35.0	9.7	226
SD	7.35	7.46	7.63	2.08	1.70	1.78	0.49	28.65
Min	150	92	87	44.3	62.0	31.5	8.4	173
Max	182	125	114	53.0	69.4	40.3	11.3	278
n	76	56	34	57	37	55	56	17
subadult								
Mean	169	113	106	48.2	66	35.2	9.7	206
SD	8.17	7.30	12.73	2.06	1.59	1.29	0.38	0.71
Min	156	102	97	45.3	64.5	33.4	9.4	205
Max	177	121	115	50.2	67.7	36.5	10.2	206
n	5	5	2	5	4	4	4	2

intermediate plumaged immature								
Mean	164	111	106	47.9	64.3	33.8	10.0	208
SD	10.22	9.88	9.42	2.88	2.32	1.59	0.35	29.57
Min	144	93	90	41.4	60.5	30.9	9.0	164
Max	178	131	125	53.7	67.7	37.5	10.6	284
n	44	44	35	44	34	44	44	32
female-plumaged immature								
Mean	167	116	109	49.5	65.1	34.2	9.8	221.1
SD	7.07	7.25	7.36	1.93	1.64	1.09	0.55	13.44
Min	148	99	95	46.7	62	32.5	7.9	187
Max	178	126	120	54.2	67.8	35.9	10.4	234
n	24	23	17	24	19	24	24	14
Females: adult								
Mean	164	116	111	46.0	63.9	34.4	10.2	208
SD	6.1	6.0	7.0	2.1	1.6	1.6	0.4	19.5
Min	145	98	91	41.5	60.1	31.0	9.2	170
Max	176	128	123	51.6	67.2	38.2	10.9	250
n	64	63	40	64	46	63	62	31

Sericulus bakeri (Chapin, 1929)
Adelbert Bowerbird
(Tables 13 and 22)

Its tail/wing length ratio is 59%, the second shortest for the family. ♀♀ average 8%, 5% and 8% larger than ♂♂ in tail and bill length and bill width, respectively, but 5% lighter in weight. In most ♀/♂ ratios, as well as tail/wing length for both sexes combined, this (dark-billed) species is more like dark-billed *Se. aureus* than pale billed *Se. ardens*. Gilliard (1969) gave the short bill length "from base" of 23 for ♂♂ and of 24 for ♀♀ (cf. Table 13) but these are probably of exposed culmen. Range: Adelbert Ra, PNG.

Sericulus chrysocephalus (Lewin, 1808)
Regent Bowerbird
(Tables 14 and 22)

Tail/wing length ratio 71%. ♀♀ average 6%, 24%, 19% and 12% larger than ♂♂ in wing and tail lengths and bill width and depth, respectively and average 23% heavier. With increasing age, ♂♂ wings and tails become relatively shorter and their mean central tail feather length gets shorter relative to tail length. As a result, the tail/wing length ratio in ♂♂ is 66% but in ♀♀ is 77%. Lenz (1999:38) gave bill length of 26.0 for ♂♂ and 25.6 for ♀♀. We concur with Hartert (1929) and Schodde & Mason (1999) in considering the doubtful northern *Se. c. rothschildi*, Mathews, 1912 invalid. Range: From N of Sydney to Connors and Clarke Ra, inland of Mackay with a gap at the Fitzroy R valley inland of Rockhampton, Australia.

Ptilonorhynchus violaceus (Vieillot, 1816)
Satin Bowerbird
(Tables 15, 16 and 22)

Tail/wing length ratio 67%, tarsus/wing length 28%, and bill/wing length 21%. ♀♀ average 6%

TABLE 16. Mean measurements of *Ptilonorhynchus v. violaceus*, from N to S of its range in latitudinally bounded subdivisions.

Degress of latitude S Sex/age group	Wing length (n, SD)	Tail length (n, SD)	Tail/wing ratio
26 - 30			
Males: adult	170 (20, 3.07)	107 (20, 4.05)	0.63
immature *	169 (12, 4.40)	114 (12, 4.77)	0.67
Females: adult	164 (9, 4.55)	114 (9, 3.71)	0.7
All birds	169 (41, 4.40)	111 (41, 5.42)	0.66
30 - 32			
Males: adult	172 (22, 3.21)	110 (3, 3.21)	0.64
immature	168 (1)	—	—
Females: adult	166 (4, 7.14)	117 (4, 5.85)	0.7
All birds	171 (27, 4.30)	114 (7, 6.08)	0.67
32 - 34			
Males: adult	174 (6, 6.63)	113 (6, 4.72)	0.65
immature *	172 (16, 3.40)	120 (16, 3.82)	0.7
Females: adult	163 (17, 3.17)	115 (16, 3.66)	0.71
All birds	168 (39, 6.17)	117 (38, 4.78)	0.7
34 - 36			
Males: adult	171 (2, 0.71)	112 (2, 3.54)	0.65
immature	169 (8, 4.34)	117 (8, 4.50)	0.69
Females: adult	166 (2, 7.07)	116 (2, 5.66)	0.7
All birds	169 (12, 4.30)	116 (12, 4.54)	0.69
36 - 39			
Males: adult	174 (10, 4.56)	115 (9, 5.52)	0.66
immature *	171 (13, 3.69)	121 (13, 4.64)	0.71
Females: adult	167 (23, 4.82)	120 (23, 3.97)	0.72
All birds	170 (46, 5.14)	119 (45, 4.85)	0.7

* Samples for 26-30 degrees include two subadults (i.e. immature showing some signs of adult plumage) and for 32-34 and 36-39 degrees one subadult each

and 8% smaller than ♂♂ in tarsus length and weight, but 7% and 5% larger in tail length and bill width. Thus ♂♂ tails become relatively shorter with increasing age. Mean bill length averages 2% shorter in ♀♀ than ♂♂, contrary to comparison of the exposed culmen (Schodde & Mason, 1999). Males in their first to third year have ♀♀-like plumage, but with whiter underparts. In their fourth to sixth year, or prior to attaining subadult characters, their plumage becomes indicative of that of ♂♂ by increasingly solid green breast and throat plumage (Disney, 1970). ♂♂ lacking adult or subadult plumage are '♀-plumaged immature ♂♂'. Birds with any sign of the more solid green breast/throat are 'intermediate-plumaged immature ♂♂'.

Ptilonorhynchus violaceus violaceus (Vieillot, 1816)

Based on the surgical sexing of 19 birds, and 3 on plumage, caught and measured at Healesville,

Victoria, it was concluded that birds with a tarsus length >57.5 and wing length >161 are ♂♂ and less are ♀♀ (Miller, 1995). Tarsus length measurements of Miller are "tarsus with foot length" of Lowe (1989), thus his are 18% larger than ours. One ♂ of our sample had a wing length of 161, and a tarsus length of 48.9. While our 60 ♀ tarsus lengths are shorter than 58, and thus agree with Miller (1995), 45 ♀♀ had a wing length of 162 or more. Range: coastal Australia in a <250 km band, narrowing to the N, from the Otway Ra W of Melbourne to Dawes Ra, Qld.

Schodde & Mason (1999) described a 'step' in size and tail proportions of the adult (I. Mason pers. comm.) populations in the centre of the range. They wrote that "Within the southern form, there is evidence of incipient divergence at the Hunter River (- Sydney) Barrier, NSW" and go on to observe that "Populations of nominotypical *violaceus* north of the Hunter to northern limits in the Dawes Range (Kroombit plateau), Qld, are relatively small with short tails (wing: ♂♂ c 167-173, ♀♀ c 157-165 mm; tail/wing ratio: ♂♂ c 0.58-0.64, ♀♀ c 0.66-0.70; n = 76). Those S of the Illawarra (Wollongong-Nowra) region are all larger and longer tailed (wing: ♂♂ c 170-178, ♀♀ c 163-170 mm; tail/wing ratio: ♂♂ c 0.63-0.67, ♀♀ c 0.68-0.72; n = 43). In between, from the Hunter to the Illawarra, populations appear to grade from one size morph to the other (n = 65)." Schodde & Mason (1999) claimed that birds N of the Hunter River (or of 32°) are "relatively small with short tails". While our data support this in broadest terms (Table 16) the differences are at best slight, and are less so in adult ♀♀ than in all ♂♂. Schodde & Mason also found birds S of 34° larger and longer tailed, but we find this true of only adult ♀ wing length, as there is little difference in tail/wing length ratio (Table 16).

Mean values for ♂ and ♀ wing length and tail length are compared using Student's two-tailed *t*-test between more pertinent pairs of the five geographical samples (Table 16). Results are as follows: there is no significance in ♂ or in ♀ wing length between the sample pairs of 30-32° and 32-34°, 32-34° and 34-36°, 30-32° and 34-36° S (all being *P* > 0.1). There is also no significance in ♂ and ♀ tail length between these same sample pairs (*P* > 0.1). Wing length between 26-30° and 36-39° S were significant (*P* < 0.02), but ♀ wing length between them was not (*P* > 0.1). Differences in ♂ and in ♀ tail length between these extremes are, however, more significant (*P* < 0.001). The latter differences are

TABLE 17. Measurements (mm) and weights (g) of *Chlamydera maculata*.

	Wing length	Tail length	Tarsus length	Total head length	Bill length	Bill width	Weight
Males: adult							
Mean	151	109	40.7	59.7	31.5	8.0	139
SD	3.29	4.12	1.56	1.06	1.47	0.46	6.25
Min	145	101	37.6	57.7	28.6	7.0	125
Max	157	117	44.5	61.4	34.9	9.0	150
n	30	30	30	21	29	30	19
subadult							
Mean	150	112	40.4	58.6	31.7	8.1	144
SD	2.6	4.2	1.4	1.0	1.1	0.5	15.5
Min	145	104	37.6	56.9	29.5	7.6	127
Max	154	120	42.5	60.0	34.0	9.1	186
n	22	22	22	11	22	22	12
immature							
Mean	152	117	40.5	58.2	31.3	7.5	117
SD	2.83		1.43		2.55	1.13	
Min	150		39.4		29.5	6.7	
Max	154		41.5		33.1	8.3	
n	2	2	2	1	2	2	1
Females: adult							
Mean	148	110	38.9	58.5	31.4	8.2	141
SD	3.44	4.10	1.10	1.47	1.47	0.33	11.71
Min	141	103	36.7	55.4	29.4	7.7	124
Max	156	117	40.8	61.6	35.4	8.9	162
n	30	30	29	26	29	30	13

not surprising, however, given they are between populations at each end of a distribution.

As it is possible that small differences apparent in some sizes for sex/age classes in Table 16 are due to small samples (e.g. for adult ♂♂ of the 32–34° and 34–36°, and adult ♀♀ of the 30–32° and 34–36°) it is worth comparing figures for all birds combined for each zone. These show little difference in wing length for the subspecies, with not even a discernable N-S cline. Our data do not indicate a cline, or step, in tail/wing length ratio with latitude. Tails are slightly longer in the S than in the N, but even between the N- and S-most zones the difference is minimal (4%) and clinal, with no obvious step (Table 16).

Ptilonorhynchus violaceus minor

A.J. Campbell, 1912

All measurements are about 10% less than in *violaceus violaceus* but body proportions are similar. Plumages are similar but the green of ♀ plumage has a dull bluish-grey cast (Schodde & Mason, 1999). Range: Australian Wet Tropics, from Mt Amos S of Cooktown to Seaview-Paluma Ra, Qld.

Table 15 shows full overlap in wing and tarsus lengths of ♀♀ within the ♂♂ range. Our bill length data (21% of wing length in *violaceus minor* and 20% in *violaceus violaceus*) do not

support the observation that the bill of *violaceus violaceus* is "long and thick" (Schodde & Mason, 1999). This difference from Schodde & Mason (1999) may be due to method of measurement. Their measurement can be misleading, particularly in dimorphic species in which only one sex has modified and/or longer plumage at the base of the upper mandible (Frith & Frith, 1997c: 173). Adult ♂♂ show *minor* to have a bill width 5% narrower than *violaceus violaceus*, and adult ♀♀ *minor* have a bill width 7% narrower than *violaceus violaceus*. For the sexes combined bill width in *minor* is 9.6 and in *violaceus violaceus* 9.9 which, given the difference in their overall sizes, is not striking. The bill of *violaceus violaceus* is not proportionately thicker than that of *minor*. In view of this, we assume Schodde & Mason (1999) meant that the bill of *violaceus violaceus* is long and deep (not thick) and thus "appears stumper in shape" but, like us, they provide no bill depth measurements. Bill width/length is the same in ♂♂ (28%) and ♀♀ (30%) of both subspecies.

Chlamydera maculata (Gould, 1837)

Spotted Bowerbird
(Tables 17 and 22)

Gilliard treated *guttata* as a subspecies of *C. maculata*, but others consider it a distinct species (Frith & Frith, 1997a; Christidis & Boles, 1994; Schodde & Mason, 1999). The tail/wing length ratio is 73%, tarsus/wing length 27%, and bill/wing length 21%. ♀♀ are fractionally smaller than ♂♂, but fractionally larger in bill width and in weight. The species is thus less sexually dimorphic in size than congeners, while being similar in major proportions (Tables 17–21). Immature ♂♂ lack crest feathers, while subadult ♂♂ have some to many. Range: Interior of Qld S of 20° S, except extreme W and SW, and interior of northern and central New South Wales (NSW) (except extreme W border country). Also extreme NW corner of Victoria and just into South Australia (SA), on the Murray R. Once confirmed to have hybridised where it meets *C. melanotos* some 100 km SSE of Charters Towers, Qld (Frith & Frith, 1995b).

Chlamydera guttata Gould, 1862

Western Bowerbird
(Tables 18 and 22)

♀♀ average fractionally smaller than ♂♂ in wing and tarsus lengths, but 5% larger in tail length and bill width, the sexes being the same in total head and bill lengths. Tail/wing length ratio

TABLE 18. Measurements (mm) and weights (g) of *Chlamydera guttata*.

	Wing length	Tail length	Tarsus length	Total head length	Bill length	Bill width	Weight
<i>C. g. guttata</i>							
Males: adult							
Mean	149	92	38.9	57.9	30.4	7.4	134
SD	2.47	3.30	1.03	0.95	0.99	0.31	5.17
Min	144	86	36.1	55.7	28.1	6.8	128
Max	157	100	41.6	59.3	32.6	7.9	142
n	34	33	34	31	34	34	8
subadult							
Mean	148	97	39.1	57.8	30.8	7.1	133
SD	1.47	4.49	1.52	0.71	0.34	0.34	4.95
Min	146	90	37.6	56.6	30.2	6.7	129
Max	150	102	41.9	58.6	31.2	7.7	136
n	6	6	6	6	6	6	2
Females: adult							
Mean	147	98	38.1	58.2	30.2	7.7	137
SD	2.36	2.70	1.21	1.24	1.17	0.36	8.20
Min	143	94	35.7	56.1	27.7	6.9	122
Max	152	104	41.0	59.9	31.9	8.4	148
n	21	21	21	17	20	19	9
<i>C. g. carteri</i>							
Males: adult							
mean	135	93	37.3		28.7	7	
n	1	1	1		1	1	
Females: adult							
Mean	137	91	36.5	57.1	30.5	7.7	
SD	2.88	3.33	0.57		0.81	0.38	
Min	135	87	35.5		29.7	7.1	
Max	141	95	37.2		32.0	8.2	
n	6	6	6	1	5	6	
All subspecies							
Males: adult							
Mean	148	92	38.9	57.9	30.4	7.3	134
SD	3.36	3.26	1.05	0.95	1.02	0.31	5.17
Min	135	86	36.1	55.7	28.1	6.8	128
Max	157	100	41.6	59.3	32.6	7.9	142
n	35	34	35	31	35	35	8
subadult							
Mean	148	97	39.1	57.8	30.8	7.1	133
SD	1.47	4.49	1.52	0.71	0.34	0.34	4.95
Min	146	90	37.6	56.6	30.2	6.7	129
Max	150	102	41.9	58.6	31.2	7.7	136
n	6	6	6	6	6	6	2
Females: adult							
Mean	145	97	37.8	58.1	30.3	7.7	137
SD	4.90	4.30	1.31	1.23	1.09	0.36	8.20
Min	135	87	35.5	56.1	27.7	6.9	122
Max	152	104	41.0	59.9	32.0	8.4	148
n	27	27	27	18	26	25	9

65%, tarsus/wing length 26%, and bill/wing length 21%, the first of these confirming the short tail (8% shorter than *C. maculata*).

This Australian taxon was treated as a separate species until Mathews (1912) considered it a subspecies of *C. maculata*. We agree with Schodde (1982) that *guttata* is a separate species. For diagnosis see Schodde & Mason (1999).

TABLE 19. Measurements (mm) and weights (g) of *Chlamydera nuchalis*.

	Wing length	Tail length	Tarsus length	Total head length	Bill length	Bill width	Weight
<i>C. n. nuchalis</i>							
Males: adult							
Mean	182	144	49.1	69.0	38.7	9.0	216
SD	5.73	6.83	1.90	1.54	1.30	0.55	27.94
Min	171	133	45.6	65.6	36.0	7.9	180
Max	193	157	54.6	71.8	40.8	10.6	265
n	35	35	35	26	34	35	9
subadult							
Mean	180	144	48.4	69.5	39.1	9.0	222
SD	4.60	5.93	1.38	1.02	1.28	0.43	12.36
Min	170	135	44.3	68.1	36.8	7.9	201
Max	189	157	49.8	72.0	41.0	9.5	240
n	17	17	17	12	16	17	9
immature							
Mean	179	151	49.2	68.9	39.0	8.5	213
SD	7.83	7.51	2.18	2.12	1.53	0.49	17.30
Min	163	138	44.4	65.2	36.5	7.4	195
Max	196	165	54.0	73.2	41.6	9.3	242
n	31	31	31	18	28	30	10
Females: adult							
Mean	173	143	45.7	66.9	37.6	8.8	186
SD	6.89	7.49	1.80	1.48	1.55	0.47	14.15
Min	158	127	42.3	64.2	32.2	7.6	164
Max	191	160	50.5	69.7	41.5	9.8	215
n	51	50	51	35	50	50	17
<i>C. n. orientalis</i>							
Males: adult							
Mean	175	131	46.9	68.5	38.4	8.9	210
SD	3.59	4.50	2.00	1.48	1.69	0.49	13.53
Min	167	122	43.1	65.4	34.5	8.2	187
Max	182	139	52.6	71.6	41.4	10.1	236
n	26	26	26	15	26	26	10
subadult							
Mean	177	134	47.4	67.6	37.8	8.8	240
SD	5.21	5.08	1.53	1.56	1.78	0.55	56.46
Min	168	124	44.6	65.9	35.2	8.1	187
Max	186	145	50.2	70.3	41.7	9.7	317
n	15	15	15	6	15	14	5
immature							
Mean	169	134	46.1	66.8	37.3	8.6	200
SD	6.98	7.38	1.92	1.22	1.54	0.51	10.67
Min	158	121	41.5	63.9	35.0	8.0	188
Max	186	149	50.7	68.1	39.9	9.8	213
n	32	32	32	11	32	32	5
Females: adult							
Mean	167	131	43.8	65.6	38.9	8.7	188
SD	5.55	5.26	1.73	1.74	1.47	0.53	15.58
Min	155	122	40.7	62.9	32.6	7.7	153
Max	177	142	46.9	67.6	38.6	9.9	205
n	33	33	33	14	32	32	13
All subspecies							
Males: adult							
Mean	179	138	48.2	68.8	38.6	9.0	212
SD	6.08	6.91	2.24	1.52	1.47	0.53	21.17
Min	167	122	43.1	65.4	34.5	7.9	180
Max	193	157	54.6	71.8	41.4	10.6	265
n	61	61	61	41	60	61	19
subadult							
Mean	179	139	47.9	68.8	38.5	8.9	228
SD	5.10	7.26	1.51	1.50	1.65	0.49	34.04
Min	168	124	44.3	65.9	35.2	7.9	187
Max	189	157	50.2	72.0	41.7	9.7	317
n	32	32	32	18	31	31	14
immature							
Mean	174	142	47.6	68.1	38.1	8.6	209
SD	8.81	11.09	2.56	2.06	1.75	0.50	16.36
Min	158	121	41.5	63.9	35.0	7.4	188
Max	196	165	54.0	73.2	41.6	9.8	242
n	63	63	63	29	60	62	15
Females: adult							
Mean	170	138	44.9	66.6	37.4	8.7	187
SD	6.86	8.71	2.01	1.65	1.57	0.49	14.56
Min	155	122	40.7	62.9	32.2	7.6	153
Max	191	160	50.5	69.7	41.5	9.8	215
n	84	83	84	49	82	82	30

TABLE 20. Measurements (mm) and weights (g) of *Chlamydera cerviniventris*.

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
Australia								
Males: adult								
Mean	140	112		41.4	61.4	30.6	7.6	175
SD	3.30	3.36		0.65	1.44	1.08	0.44	4.73
Min	141	105		39.4	58.7	28.4	6.8	170
Max	154	116		42.9	62.9	32.1	8.7	182
n	24	24		24	5	22	23	7
Females: adult								
Mean	144	111	104	39.1	60.4	30.5	8.1	157
SD	3.96	3.71		1.42	1.02	1.03	0.31	9.78
Min	138	104		36.8	59.1	28.4	7.6	144
Max	150	118		41.5	61.8	32.7	8.5	167
n	19	17	1	16	6	17	19	5
New Guinea								
Males: adult								
Mean	149	111	106	41.0	59.6	30.8	8.2	159
SD	4.15	2.69	2.07	1.43	5.61	1.15	0.4	10.66
Min	141	107	104	39.4	39.6	28.1	7.4	145
Max	157	117	109	43.3	64.2	33.7	9.1	180
n	37	35	6	35	32	36	35	37
Females: adult								
Mean	146	111	106	39.3	60.5	30.9	8.3	149
SD	4.02	2.97	2.43	1.42	1.44	1.14	0.69	13.65
Min	139	105	104	34.7	57.2	29.0	7.0	117
Max	155	119	110	42.2	63.5	34.9	10.5	170
n	32	32	5	33	29	33	33	16
All birds								
Males: adult								
Mean	148	112	106	41.2	60.1	30.7	8.0	162
SD	3.61	2.69	2.07	1.23	5.20	1.13	0.50	11.46
Min	141	105	104	38.4	39.6	28.1	6.8	145
Max	157	118	109	43.3	64.2	33.7	9.1	182
n	61	60	6	59	38	58	58	44
Females: adult								
Mean	145	111	106	39.3	60.5	30.8	8.2	151
SD	4.10	3.22	2.40	1.41	1.37	1.10	0.58	13.19
Min	138	104	104	34.7	57.2	28.4	7.0	117
Max	156	119	110	42.2	63.5	34.9	10.5	170
n	91	89	6	91	75	86	86	57

Chlamydera guttata guttata Gould, 1862

The larger subspecies, blacker dorsally and with a longer and broader nuchal crest. ♂♂ have crests and ♀♀ vary from no crest to a complete one. Range: Western Australia (WA), from the base of North West Cape through the Pilbara and into the central interior. Thence E in a narrowing band, across the Northern Territory (NT) border into the S of NT to c. 200–300 km N and E of Alice Springs, and extending 100 km S of the NT/SA border and E to due S of Alice Springs.

Chlamydera guttata carteri Mathews, 1920

Averages 8% smaller in wing length and 5% in tarsus length than the nearest populations of *guttata guttata* (Hammersley R, Onslow & Sherlock R areas) but only fractionally so in tail and bill lengths. Thus *carteri* has a long (and

broad) bill, in addition to being richer and more russet coloured than *guttata guttata* (Frith & Frith, 1997a). Five of six ♀♀ examined have a full ♂-like crest. Range: Restricted to North West Cape, WA.

Chlamydera nuchalis (Jardine & Selby, 1830) Great Bowerbird (Tables 19 and 22)

Adults have tail/wing length ratio 79%, tarsus/wing length 27%, bill/wing length 22%. ♀♀ average 5%, 7% and 12% smaller than ♂♂ in wing and tarsus lengths and weight, respectively. All adult ♂♂ have a full crest, and the 17 subadult ♂♂ have between 10 crest feathers to three-quarters of a full ♂-like crest. Of 84 ♀♀, none have a full ♂-like crest while 4 have only 4–10 crest feathers, 2 a quarter-developed crest, 3 a third-, 1 a half-, and 1 a three-quarter developed crest (Frith & Frith, 1999).

Chlamydera nuchalis nuchalis (Jardine & Selby, 1830)

Chlamydera nuchalis owenii Mathews, 1912.

The larger subspecies. ♀♀ average 5% smaller than ♂♂ in wing length, 7% smaller in tarsus length and 14% lighter. Mean ratios for sexes combined are: tail/wing length 81%, tarsus/wing 27%, bill/wing 22%. We agree with Mayr & Jennings (1952), Gilliard (1969) and Hall (1974) that this subspecies has paler and less contrasting, more uniform and greyish, upperparts and underparts usually darker than *orientalis*. Immatures exhibit slight and faint ventral (mostly flank) barring (stronger in some more W individuals), but adults less so or not at all. Adults typically lack silky silvery-white feather tipping, or spotting, throughout the crown (and when present only about the pink nuchal crest feathers). Range: Kimberley, NT, extreme NW Qld, islands off N coast, to no further S than 20° S.

Chlamydera nuchalis orientalis Gould, 1879

Chlamydera nuchalis yorki Mayr & Jennings, 1952.

The smaller subspecies, averaging 9% smaller in tail length, and fractionally so in tarsus and bill lengths and bill width than *nuchalis nuchalis*. Similar to *nuchalis nuchalis* in ♀ size as proportion of. Mean combined sexes tarsus/wing length and bill/wing length ratios the same as *nuchalis nuchalis*, but tail/wing 77% (Frith & Frith, 1999). Dorsal colouration and markings (Mayr & Jennings, 1952) are darker and more variegated or contrasting in pattern. Ventral

TABLE 21. Measurements (mm) and weights (g) of *Chlamydera lauterbachii*.

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
<i>C. l. lauterbachii</i>								
Males: adult								
Mean	133	104		39.7	57.0	27.5	6.9	135
SD	1.41	2.83		0.21	1.70		0	
Min	132	102		39.5	26.3		6.9	
Max	134	106		39.8	28.7		6.9	
n	2	2		2	1	2	2	1
<i>C. l. uniformis</i>								
Males: adult								
Mean	134	106	99	38.6	56.3	28.1	6.9	130
SD	2.67	3.39		1.59	1.51	0.87	0.29	3.89
Min	130	100		34.8	52.6	26.3	6.4	128
Max	139	112		41.4	57.8	29.6	7.5	133
n	21	20	1	22	10	22	21	2
Females: adult								
Mean	131	106	102	37.5	56.6	28.2	7.2	115
SD	2.82	4.25	1.73	1.47	1.29	0.69	0.34	4.16
Min	125	99	100	35.3	53.9	26.6	6.2	112
Max	137	116	103	41.1	58.2	29.5	7.8	120
n	26	26	3	26	12	26	26	3
All subspecies								
Males: adult								
Mean	134	106	99	38.7	56.3	28.0	6.9	132
SD	2.58	3.34		1.55	1.45	0.92	0.27	3.88
Min	130	100		34.8	52.6	26.3	6.4	128
Max	139	112		41.4	57.8	29.6	7.5	135
n	23	22	1	24	11	24	23	3
Females: adult								
Mean	131	106	102	37.5	56.6	28.2	7.2	115
SD	2.82	4.25	1.73	1.47	1.29	0.69	0.34	4.16
Min	125	99	100	35.3	53.9	26.6	6.2	112
Max	137	116	103	41.1	58.2	29.5	7.8	120
n	26	26	3	26	12	26	26	3

plumage, particularly flanks, usually strongly barred. Birds in the NE (formerly *yorki*) average slightly smaller and paler, more so ventrally and particularly on the throat, than those to the S (Frith & Frith, 1999). Range: Qld N of 20° S, a little further S in the E. Absent on Cardwell-Tully coast and E watershed of the Wet Tropics ranges. Locally sympatric with *C. cerviniventris* on NE Cape York Peninsula, but hybrids unknown.

Gilliard (1969) followed Mayr & Jennings (1952) in accepting 4 subspecies. Now *oweni* is considered a synonym of *nuchalis* and *yorki* is synonymous with *orientalis* (Frith & Frith, 1999; Schodde & Mason, 1999). Colouration and pattern of the crown are important discriminators in *Ailuroedus*, *Amblyornis* and *Chlamydera* (Gilliard, 1969; Frith & Frith, 1995b, 1997a,b, 1998). The marked difference in crown and dorsal plumage colouration and pattern separate *nuchalis*, in WA and the NT east to the Gulf of Carpentaria in W Qld from *orientalis* in the E and

NE of Australia (Storr, 1967, 1973, 1977, 1980, 1984; Ford, 1974, 1987; Schodde, 1986). See *C. maculata* (above) for details of hybridisation.

***Chlamydera cerviniventris* Gould, 1850**
Fawn-breasted Bowerbird
(Tables 20 and 22)

There is negligible difference between NG and Qld populations (Table 20). Tail/wing length ratio is 76%, tarsus/wing length 27%, and bill/wing length 21%. ♀♀ average 5% smaller in tarsus length and are 7% lighter than ♂♂. Range: PNG coast to 500 m asl, to Humboldt Bay in N and Marauke in the S of WP. Jimi Valley, PNG at 1700 m (Frith, 1987). Locally sympatric with Lauterbach's but hybrids unknown. Isolated populations in Ransiki and Kebor Valleys of E Vogelkop; along eastern coastal zone of Cape York Peninsula to Coen, Qld where locally sympatric with Great Bowerbird but hybrids unknown.

***Chlamydera lauterbachii* Reichenow, 1897**
Lauterbach's Bowerbird
(Tables 21 and 22)

Tail/wing ratio of 80%, tarsus/wing 29%, and bill/wing 21%; ♀♀ 13% lighter than ♂♂.

Chlamydera lauterbachii lauterbachii
Reichenow, 1897

Known from two specimens, with coppery coloured crown and cheek feathering having a *Sericulus*-like metallic rose-golden sheen to it. Range: Aiome area of upper Ramu R, PNG, possibly also near Bogadjim, Finisterre Mts, PNG (Gilliard & LeCroy, 1968).

Chlamydera lauterbachii uniformis
Rothschild, 1931

No differences between this and *lauterbachii lauterbachii* in average sizes or body proportions. Crown yellowish olive-green (50). Range: NG lowlands to 1800m asl, from Geelvink Bay, WP to Okapa-Aiyura area of E Highlands, PNG. Patchy in Snow and Star Mts to upper Ramu R. Sympatric with *C. cerviniventris* SE of Hupai, Ramu Valley, and in Aiyura Valley (Bailey, 1992; Doyle et al., 1981), but hybrids unknown.

CONCLUSIONS

It has been stated that sexual size dimorphism, expressed by the ♂/♀ wing length, is no greater in polygynous bowerbirds than in monogamous *Ailuroedus* species (Payne, 1984). Polygynous *Sc. dentirostris* is, however, less sexually

TABLE 22. Mean size and some mean body proportions of adult ♀ vs ♂ bowerbirds, expressed as % ♀ are smaller than ♂ or as a % of mean size the former trait is of the latter. Values of less than 5% are not indicated. Tables 1-21 give sample sizes. MWL = mean wing length; MTL = mean tail length; MLL = mean tarsus length; MBL = mean bill length; MBW = mean bill width; MBD = mean bill depth; MW = mean weight.

Species	FEMALE/MALE							MTL/MWL (male, female)		
	MWL	MTL	MLL	MBL	MBW	MBD	MW	MLL/MWL	MBL/MWL	
<i>Al. buccoides</i>		5*	5	5	6	7	9	66 (67, 66)	28	22
<i>Al. crassirostris</i>	-		-				10	74 (74, 74)	28	20
<i>Al. melanotis</i>	-	-	-	-	5	5	8	73 (73, 73)	29	23
<i>Sc. dentiostrius</i>		-	-	-	-	-	7+	70 (70, 69)	21	21
<i>Ar. papuensis</i>	8	22	9	-	-	-	-	96 (103, 88)	26	21
<i>Am. inornatus</i>	-	-	-	-	-		5	70 (71, 70)	27	23
<i>Am. macgregoriae</i>	-	-	-	-	9		-	65 (65, 65)	27	21
<i>Am. subalaris</i>	-	-	-	-		-	-	70 (70, 70)	28	21
<i>Am. flavifrons</i>	-	-	-	-	-	-	-	62 (62, -)	25	22
<i>Pr. newtoniana</i>	-	20	-	-	13+	7+	15+	82 (90, 74)	25	19
<i>Se. aureus</i>	-	5+	-	-	7+	7	6	60 (59, 62)	29	22
<i>Se. ardens</i>	-	14+	-	-	5+	-	-	50 (47, 52)	30	21
<i>Se. bakeri</i>	-	8+	-	7+	8+	-	5	59 (57, 61)	30	22
<i>Se. chrysocephalus</i>	6+	24+	-	-	19+	12+	23+	71 (66, 77)	26	23
<i>Pt. violaceus</i>	-	7+	6	-	5+	-	8	67 (64, 71)	28	21
<i>C. maculata</i>	-	-		-		-	-	73 (72, 74)	27	21
<i>C. guttata</i>	-	5+	-	-	5+	-	-	65 (62, 67)	26	21
<i>C. nuchalis</i>	5	-	7		-	-	12	79 (77, 81)	27	22
<i>C. cerviniventris</i>	-	-	5	-	-	-	6	76 (76, 77)	27	21
<i>C. lauterbachii</i>	-	-	-	-	-	-	13	80 (79, 81)	29	21
Mean of mean ratios								71	27	21

dimorphic in size than *Ailuroedus* (Tables 1-4, 22). Our wing length data agree with Payne (1984) in demonstrating *Ar. papuensis* to be the most sexually dimorphic bowerbird in this trait. They also agree with Lenz (1999) in showing *Se. chrysocephalus* to be the second most sexually dimorphic (but reversed, in that ♀♀ are larger than ♂♂) and not the least dimorphic bowerbird (pace Payne, 1984). In all polygynous bowerbird genera except *Sericulus* ♀♀ are typically shorter in wing and tarsus lengths than ♂♂. In all bill dimensions ♀♀ *Ailuroedus* average slightly smaller than ♂♂, whereas in the majority of polygynous species ♀♀ have bills the same size or larger than ♂♂. We consider the morphology and geographical isolation of *Al. crassirostris* supportive of its distinct status from *Al. melanotis*, this being in harmony with the separation of *Se. ardens* and *C. guttata*.

ACKNOWLEDGEMENTS

For access to collections in their care we thank the staff, too numerous to mention, of the mainland Australia State Museums and the following institutions: Australian National Wildlife Collection, CSIRO, Canberra; Australian Bird and Bat Banding Scheme, Canberra; American Museum of Natural History; The Natural History Museum, Tring; National Museums and Galleries on Merseyside, Liverpool; Museum of Vertebrate Zoology, University of California, Berkeley; The Field Museum, Chicago; Museum of Comparative Zoology, Cambridge; Bishop Museum, Honolulu; Royal Ontario Museum; Academy of Natural Sciences, Philadelphia; Carnegie Museum of Natural History, Pittsburgh; Peabody Museum, Yale University; Delaware Museum of Natural History, Wilmington; Museum Zoologicum Bogoriense, Bogor; National

Museum and Art Gallery of Papua New Guinea, Port Moresby; Museo Nacional de Ciencias Naturales, Madrid; Museo Civico, Genova; Nationaal Natuurhistorisch Museum, Leiden; Swedish Museum of Natural History, Stockholm; Zoologisk Museum Københavns Universitet, København; Museum National d'Histoire Naturelle, Paris; Staatliches Museum für Tierkunde, Dresden; Zoologische Staatssammlung, München; Zoologisches Museum, Berlin; Museum Alexander Koenig, Bonn; Staatliches Museum für Naturkunde, Stuttgart; Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt; Zoologisches Institut und Zoologisches Museum, Hamburg. People who kindly provided help in other ways include Joan Airey, Brian and Del Coates, Jeff and Barbara Davies, Paul and Luisa Frith, Peter and Daphne Fullagar, Andrew and Trish Gillison and Peter and Janet Marsack. Sincere thanks to the Chapman Fund Committee for support. We thank Ian McAllan, Walter Boles, Norbert Lenz, Wayne Longmore, and an anonymous referee. Opinions expressed are ours alone.

LITERATURE CITED

- BAILEY, S.F. 1992. Bird observations in lowland Madang Province. *Muruk* 5: 111-13.
- BEEHLER, B.M. & FINCH, F. W. 1985. Species-Checklist of the birds of New Guinea. Royal Australasian Ornithologists Union Monographs 1: 1-127.
- BEEHLER, B. M., PRATT, T. K., & ZIMMERMAN, D. A. 1986. Birds of New Guinea. (Princeton University Press: Princeton).
- BORGIA, G. 1986. Sexual selection in bowerbirds. *Scientific American* 254, 70-79.
1995. Why do bowerbirds build bowers? *American Scientist* 83: 542-547.
- CHRISTIDIS, L. & BOLES, W.L. 1994. The taxonomy and species of birds of Australia and its Territories. Royal Australasian Ornithologists Union Monograph 2: 1-112.
- CHRISTIDIS, L. & SCHODDE, R. 1992. Relationships among the birds-of-paradise (Paradisaeidae) and bowerbirds (Ptilonorhynchidae): protein evidence. *Australian Journal of Zoology* 40: 343-353.
- COATES, B.J. 1990. The Birds of Papua New Guinea including the Bismarek Archipelago and Bougainville. (Dover: Brisbane).
- COLLAR, N.J. 1986. Red data bird, the Tomba Bowerbird. *World Birdwatch* 8: 5.
- COOPER, W.T. & FORSEY, J.M. 1977. The birds of paradise and bower birds. (Collins: Sydney).
- DIAMOND, J. M. 1969. Preliminary results of an ornithological exploration of the north coastal range, New Guinea. *American Museum Novitates* 2362: 1-57.
1972. Avifauna of the Eastern Highlands of New Guinea. Publication of the Nuttall Ornithological Club 12: 1-438.
1982. Rediscovery of the Yellow-fronted Gardener Bowerbird. *Science* 216: 431-434.
1985. New distributional records and taxa from the outlying mountain ranges of New Guinea. *Emu* 85: 65-91.
1986. Biology of the birds of paradise and bowerbirds. *Annual Review of Ecology and Systematics* 17: 17-37.
1987. Bower building and decoration by the bowerbird *Amblyornis inornatus*. *Ethnology* 74: 177-204.
- DISNEY, H.J.de S. 1970. Bird in the hand. Satin Bowerbird (*Ptilonorhynchus violaceus*). *Australian Bird Bander* 8: 12-13.
- DONAGHEY, R.H. 1996. Bowerbirds. In Strahan, R. (ed.). *Finches, bowerbirds & other passerines of Australia*. (Angus & Robertson: Sydney).
- DOYLE, G., DOYLE, D., STRINGER, M., FABB, C., SANDERSON, C., FOREMAN, V., & MARTEN, H. 1981. Birds of the Aiyura Valley. (Department of Education Papua New Guinea: Port Moresby).
- FORD, J. 1974. Speciation in Australian birds adapted to arid habitats. *Emu* 74: 161-168.
1977. Taxonomic status of the Spotted Catbird on Cape York Peninsula. *Sunbird* 8: 61-64.
1987. Hybrid zones in Australian birds. *Emu* 87: 158-178.
- FRITH, C.B. 1970. Sympatry of *Amblyornis subalaris* and *A. macgregoriae* in New Guinea. *Emu* 70: 196-197.
1987. Fawn-breasted Bowerbird *Chlamydera cerviniventris* on the Laj River, Jimi Valley, Western Highlands, Papua New Guinea. *Muruk* 2: 63.
- FRITH, C.B. & BEEHLER, B.M. 1998. The birds of paradise: Paradisaeidae. (Oxford University Press: Oxford).
- FRITH, C. B. & FRITH, D.W. 1989. Miscellaneous notes on the bowerbirds *Chlamydera cerviniventris* and *C. lauterbachii* (Ptilonorhynchidae) in Papua New Guinea. *Australian Bird Watcher* 13: 6-19.
1990. Archbold's Bowerbird *Archboldia papuensis* (Ptilonorhynchidae) uses plumes from King of Saxony Bird of Paradise *Pteridophora alberti* (Paradisaeidae) as bower decoration. *Emu* 90: 136-137.
1993. Courtship display of the Tooth-billed Bowerbird *Scenopoeetes dentirostris*: its behavioural and systematic significance. *Emu* 93: 129-136.
1994. Courts and seasonal activities at them by male Tooth-billed Bowerbirds *Scenopoeetes dentirostris* (Ptilonorhynchidae). *Memoirs of the Queensland Museum* 37: 21-145.
- 1995a. Court site constancy, dispersion, male survival and court ownership in the male

- Tooth-billed Bowerbird, *Scenopoeetes dentirostris* (Ptilonorhynchidae). *Emu* 95: 84-98.
- 1995b. Hybridization between the Great and Spotted Bowerbird *Chlamydera nuchalis* and *C. maculata*, the first authenticated hybrid bowerbird (Ptilonorhynchidae). *Memoirs of the Queensland Museum* 38: 471-476.
- 1997a. *Chlamydera guttata carteri* - an overlooked subspecies of Western Bowerbird (Ptilonorhynchidae) from North West Cape, Western Australia. *Records of the Western Australian Museum* 18: 219-226.
- 1997b. A distinctive new subspecies of Macgregor's Bowerbird (Ptilonorhynchidae) of New Guinea. *Bulletin of the British Ornithologists' Club* 117: 199-205.
- 1997c. Biometrics of birds of paradise (Aves: Paradisaeidae): with observations on interspecific and intraspecific variation and sexual dimorphism. *Memoirs of the Queensland Museum* 42: 159-212.
1998. Hybridization between Macgregor's Bowerbird *Amblyornis macgregoriae* and the Streaked Bowerbird *A. subalaris* (Ptilonorhynchidae) of New Guinea. *Bulletin of the British Ornithologists' Club* 118: 7-14.
1999. Subspeciation in the Australian-endemic Great Bowerbird *Chlamydera nuchalis* (Ptilonorhynchidae): a review and revision. *Bulletin of the British Ornithologists' Club* 119: 177-189.
- 2000a. Bower system and structures of the Golden Bowerbird, *Prionodura newtoniana* (Ptilonorhynchidae). *Memoirs of the Queensland Museum* 45: 293-316.
- 2000b. Attendance levels and behaviour at bowers by male Golden Bowerbirds, *Prionodura newtoniana* (Ptilonorhynchidae). *Memoirs of the Queensland Museum* 45: 317-341.
- 2000c. Home range and associated sociobiology and ecology of male Golden Bowerbirds *Prionodura newtoniana* (Ptilonorhynchidae). *Memoirs of the Queensland Museum* 45: 343-357.
- 2000d. Fidelity to bowers, adult plumage acquisition, longevity and survival in male Golden Bowerbirds *Prionodura newtoniana*. *Emu* 100: 249-263.
- FRITH, C.B., GIBBS, D. & TURNER, K. 1995. The taxonomic status of populations of Archbold's Bowerbird *Archboldia papuensis* in New Guinea. *Bulletin of the British Ornithologists' Club* 115: 109-114.
- GILLIARD, E.T. 1951. New Guinea's paradise of birds. *National Geographic Magazine* 100: 661-688.
1958. *Living birds of the world*. (Hamish Hamilton: London).
1959. A comparative analysis of courtship movements in closely allied bowerbirds of the genus *Chlamydera*. *American Museum Novitates* 1936: 1-8.
1963. The evolution of bowerbirds. *Scientific American* 209: 38-46.
1969. *Birds of paradise and bowerbirds*. (Weidenfeld & Nicolson: London).
- GILLIARD, E.T. & LECROY, M. 1968. Birds of the Schröder Mountain Region, New Guinea. Results of the American Museum of Natural History Expedition to New Guinea in 1964. *American Museum Novitates* 2343: 1-41.
- HALL, B.P. (ed.) 1974. *Birds of the Harold Hall Australian Expeditions 1962-1970*. (British Museum (Natural History): London).
- HARTERT, E. 1929. Types of birds in the Tring Museum. D. Gregory M. Mathews's types of Australian birds. I Dromiciidae-Paradisaeidae. *Novitates Zoologicae* 35: 42-58.
- JOHNSGARD, P.A. 1994. *Arena birds - sexual selection and behaviour*. (Smithsonian Institution Press: Washington).
- KUSMIERSKI, R., BORGIA, G., CROZIER, R.H. & CHAN, B.H.Y. 1993. Molecular information on bowerbird phylogeny and the evolution of exaggerated male characteristics. *Journal of Evolutionary Biology* 6: 737-752.
- KUSMIERSKI, R., BORGIA, G., UY, A., & Crozier, R.H. 1997. Labile evolution of display traits in bowerbirds indicates reduced effects of phylogenetic constraint. *Proceedings of the Royal Society of London B*, 264: 307-313.
- LENZ, N. 1999. Evolutionary ecology of the Regent Bowerbird *Sericulus chrysocephalus*. *Ökologie der Vögel* 22 (Supplement): 1-200.
- LOWE, K. W. 1989. *The Australian bird bander's manual*. Australian bird and bat banding scheme. (ANPWS: Canberra).
- MACK, G. 1953. Birds from Cape York Peninsula, Queensland. *Memoirs of the Queensland Museum* 13: 1-39.
- MACKAY, R. 1984. Short note on a bird of paradise and a bower bird. *Papua New Guinea Bird Society Newsletter* 209: 4-5.
- MATHEWS, G.M. 1912. A reference-list to the birds of Australia. *Novitates Zoologicae* 18: 171-455.
1941. Two new subspecies of birds collected by Dr. Scott at Cape York. *Emu* 40: 384.
- MAYR, E. & JENNINGS, K. 1952. Geographic variation and plumages in Australian bowerbirds. *American Museum Novitates* 1602: 1-18.
- MEES, G.F. 1964. Four new subspecies of birds from the Moluccas and New Guinea. *Zoologische Mededelingen* 40: 25-130.
1965. The avifauna of Misool, Nova Guinea. *Zoology* 31: 139-203.
1982. Birds from the lowlands of southern New Guinea (Merauke and Koembe). *Zoologische Verhandlungen* 191: 1-188.
- MILLER, M.A. 1995. Size differences in male and female 'green' Satin Bowerbirds *Ptilonorhynchus violaceus*. *Corella* 19: 146-148.

- NIX, H.A. & SWITZER, M.A. 1991. Rainforest animals - atlas of vertebrates endemic to Australia's Wet Tropics. Kowari 1: 1-112.
- PAYNE, R.B. 1984. Sexual selection, lek and areana behaviour, and sexual size dimorphism in birds. Ornithological Monographs 33: 1-52. (American Ornithologists' Union: Washington).
- PECKOVER, W.S. & FILEWOOD, L.W.C. 1976. Birds of New Guinea and Tropical Australia. (Reed: Sydney).
- PIZZEY, G. 1980. A field guide to the birds of Australia. (Collins, Sydney).
1997. The Graham Pizzey & Frank Knight field guide to the birds of Australia. (Angus & Robertson: Sydney).
- PRATT, T.K. 1982. Additions to the avifauna of the Adelbert Range, Papua New Guinea. Emu 82: 117-125.
- RAND, A.L. & GILLIARD, E.T. 1967. Handbook of New Guinea birds. (Weidenfeld & Nicolson: London).
- SCHODDE, R. 1976a. Evolution in the birds-of-paradise and bowerbirds, a resynthesis. Pp. 137-149. In Proceedings of the 16th International Ornithological Congress. (Australian Academy of Science: Canberra).
- 1976b. Reader's Digest complete book of Australian birds. (Reader's Digest: Sydney).
1982. Origin, adaptation and evolution of birds in arid Australia. Pp. 191-224 In W.R. Barker and P.J.M. Greenslade (Eds). Evolution of the flora and fauna of arid Australia. (Peacock Press: Adelaide).
1986. Reader's Digest complete book of Australian birds. 2nd edition. (Reader's Digest: Sydney).
- SCHODDE, R. & MCKEAN, J.L. 1973. Distribution, taxonomy and evolution of the gardener bowerbirds *Amblyornis* spp in eastern New Guinea with descriptions of two new subspecies. Emu 73: 51-60.
- SCHODDE, R. & MASON, I. 1999. The directory of Australian birds. (CSIRO: Melbourne).
- SIMPSON, K. (ed.) 1984. The birds of Australia. (Lloyd O'Neil: Adelaide).
1999. Field guide to the birds of Australia. 6th ed. (Penguin: Melbourne).
- SLATER, P. 1974. A field guide to Australian birds'. (Rigby: Adelaide).
- SLATER, P., SLATER, P. & SLATER, R. 1989. The Slater field guide to Australian birds. Revised ed. (Weldon: Sydney).
- SMITHIE, F.B. 1975. Naturalist's color guide. (American Museum of Natural History: New York).
- STORR G.M. 1967. List of Northern Territory birds. Special Publication of the West Australian Museum 4: 1-90.
1973. List of Queensland birds. Special Publication of the West Australian Museum 5: 1-177.
1977. Birds of the Northern Territory. West Australian Museum Special Publication 7: 1-130.
1980. Birds of the Kimberley Division, Western Australia. West Australian Museum Special Publication 11: 1-71.
1984. Revised list of Queensland birds. Records of the West Australian Museum, Supplement 19: 1-189.
- UY, J.A.C. & BORGIA, G. 2000. Sexual selection drives rapid divergence in bowerbird display traits. Evolution 54: 273-278.

WESTERN PACIFIC TINGIDAE (HETEROPTERA): NEW SPECIES AND NEW RECORDS

ERIC GUILBERT

Guilbert, F. 2001 06 30: Western Pacific Tingidae (Heteroptera): new species and new records. *Memoirs of the Queensland Museum* 46(2): 543-554, Brisbane. ISSN0079-8835.

Nine new species are described from the Western Pacific, namely, *Cysteochila kraussi*, *Leptoptyx varians*, *L. longispina*, *Nesocypselas simplex*, *N. strophii* from Solomon Islands, *Eteoneus samoensis* from American Samoa, *E. palauensis* from Palau Islands, *Idiocysta vanuana* from Fiji, *Onoplax majorcarinae* from Bonin Islands. Twenty other species are reported from Western Pacific islands (Bonin, Fiji, Marianas, Palau, Samoa, Society, Solomons, Tonga Islands) with comments about their distribution. □ *Tingidae. Heteroptera. Western Pacific islands. taxonomy.*

Muséum National d'Histoire Naturelle, ESA 8043, Laboratoire d'Entomologie, 45 rue Buffon, F-75231 Paris cedex 05 France (e-mail: guilbert@mnhn.fr); 31 January 2000.

This paper deals with lace bugs (Heteroptera: Tingidae) from Bonin, Fiji, Marianas, Palau, Samoa, Society, Solomons and Tonga Islands. The first species described from the region was *Tingis irregularis* (Montrouzier, 1861) from New Caledonia. By 1956 Tingidae of Micronesia (Bonin, Volcano, Mariana, Caroline Marshall and Gilbert Islands) had reached 20 species (Drake, 1965). Since then it has risen to 81 species of which about 70% were described by Drake, Poor & Ruhoff between 1943 and 1966. I added 9 species (Guilbert 1997a, 1997b, 1998a, 1998b) to this list and 9 for Vanuatu (Guilbert, 1999). Herein, 29 species are recorded from Bonin, Fiji, Marianas, Palau, Samoa, Society, Solomons and Tonga. Nine are new, namely, *Cysteochila kraussi*, *Nesocypselas simplex*, *N. strophii*, *Leptoptyx varians*, *L. longispina* from Solomon Islands, *Eteoneus samoensis* from American Samoa, *E. palauensis* from Palau, *Idiocysta vanuana* from Fiji, *Onoplax majorcarinae* from Bonin. Repositories mentioned are Bernice P. Bishop Museum, Honolulu (BPBM), Natural History Museum, London (NHM), Muséum National d'Histoire Naturelle, Paris (MNHN) and National Museum of Natural History, Washington (NMNH).

Abbreviations for collectors are: J.L. Gressitt (JG); N.H.L. Krauss (NK); T.C. Maa (TM); C.W. O'Brien (CO); C.W. Sabrosky (CS); R. Straatman (RS); G.A. & S.L. Samuelson (GSS); C.M. Yoshimoto (CY); B.H. Gagne (BG); W.C. Cagne (WG); E.C. Zimmerman (EZ); J.M. Sedlacek (JS); E.S. Brown (EB); S.N. Lal (SL); C.H. Swezey (CH); W.R. Kallen (WK); J.A. Listinger (JL); M.K. Kamath (MK); R.G. Oakley

(RO); J.W. Beardsley (JB); F.M. Snyder (FS); W. Mitchell (WM).

SYSTEMATICS

Order HEMIPTERA
Suborder HETEROPTERA
Family TINGIDAE

Cysteochila Stål, 1873

Cysteochila comprises around 135 species, and has a widespread distribution; 12 species are known from the Indo-Pacific region: 4 are known from the Solomon Islands: *C. kraussi*, *C. idonea* Drake, 1956, *C. consanguinea* (Distant, 1909), and *C. prata* Drake & Ruhoff, 1965.

Cysteochila kraussi sp. nov. (Fig. 1)

HOLOTYPE: SOLOMON ISLANDS: ♀, Poitea, Kolombangara, 0-60m, 29.xi.1976, NK, BPBM.

ETYMOLOGY. For the collector.

DESCRIPTION. Head, antennae, abdomen black, legs brown fuscous, pronotum and hemelytra brown yellowish. Body 3.70mm long, 1.08mm wide. Head short, with 2 long, inwardly curved occipital spines, 2 short straight frontal spines and stout, tubercle-like median spine. Antennae slender, I: 0.15, II: 0.14, III: 0.79, IV: 0.46, longer than first 2 together, pilose. Bucculae broad, with 3 rows of areolae, closed anteriorly; labium short, reaching middle of mesosternum; labial sulcus sinuate, narrow, open posteriorly.

Pronotum broader than hemelytra, gibbose, deeply punctate, tricarinate, carinae straight, uniseriate; areolae small. Collar moderately large, 6 areolae wide transversely on top, slightly



FIG. 1. *Cysteochila kraussi* sp. nov., habitus.

raised to form a tectiform hood not covering head. Paranota large, 8 areolae broad, reflexed inwards, resting on the pronotum, not joining on top but covering lateral carinae and not reaching median carina; areolae small, round.

Hemelytra narrow, longer than body; costal area narrow, straight, margins reflexed upwards, uniseriate, areolae small; subcostal area narrow, mostly biseriate, areolae small; discoidal area large, 6-7 areolae across, areolae small but larger than on costal and subcostal areas; sutural area 11 areolae wide, areolae moderately large, larger at apex; hypocostal laminae uniseriate.

REMARKS. *C. kraussi* differs from *C. nativa* Drake, 1960 by being smaller, and by having paranota not joining dorsally and subcostal area mostly biseriate. It differs from *C. jimmina* Drake, 1960 (New Britain and New Guinea) by the paranota not meeting on top, costal area width and the number of areolae on the costal area,

which is 1-2 areolae wide for *C. jimmina*. It differs from *C. brunnea* Hacker, 1928 (Queensland) by the shorter labium (reaching the meso-metasternal suture in *C. brunnea*), paranota not meeting dorsally, labium length and coloration.

***Cysteochila prata* Drake & Ruhoff, 1965**

NEW RECORDS. SOLOMON ISLANDS: 1 ♂, Kolombangara, Pepele, 30m, 15.III.1964, PS, BPBM.

REMARKS. *C. prata* is known from New Guinea. This is the first record of this species from the Solomon Islands.

***Cysteochila idonea* Drake, 1956**

NEW RECORDS. SOLOMON ISLANDS: 2 ♀, 2 ♂ Guadalcanal, Honiara, 0-100m, NK, BPBM1985.163; 1 ♀, Kolombangara, Gizo, 0-140m, XII.1980, NK, BPBM1981.79.

REMARKS. *C. idonea* is known from NE New Guinea, Kusaie (the Caroline Islands) and the Solomon Islands.

***Cysteochila vitilevuana* Drake & Poor, 1943**

NEW RECORDS. FIJI: ♂ Viti Levu, Namosi Rd, 6km N Queens Hwy, 250m, 3-7.XI.1981, BG, BPBM1981.601; 1 ♂, 1 ♀, 90km E of Tavua, 28.VII.1967, JS, BPBM; 1 ♂ 5 ♀, Vanua Levu, Nakawanga, 9.X.1955, JG; 1 ♀ Vanua Levu, Nakorocau, 23.III.1966, NK, BPBM.

REMARKS. *C. vitilevuana* is known only from Fiji, but is recorded here for the first time from Vanua Levu.

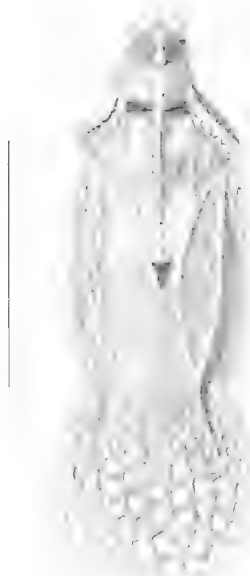
***Leptoptyx* Drake & Ruhoff, 1965**

Previously known from *atopia* and *icelia* from Solomon Islands and New Britain and following Drake & Ruhoff (1965), *Leptoptyx* is allied to *Leptopharsa* Stål 1873, but separated by its reflexed paranota, and longer and tectiform hood. *Leptoptyx* generally resembles *Trachypeplus* Horváth, 1926. Both have reflexed paranota, but *Trachypeplus* has spines on the pronotum and hemelytra, and wider hemelytra.

***Leptoptyx varians* sp. nov.**
(Fig. 2)

HOLOTYPE. SOLOMON ISLANDS: ♂, Honiara, Guadalcanal, 0-200 m, xi.1976, NK, BPBM1977.29.

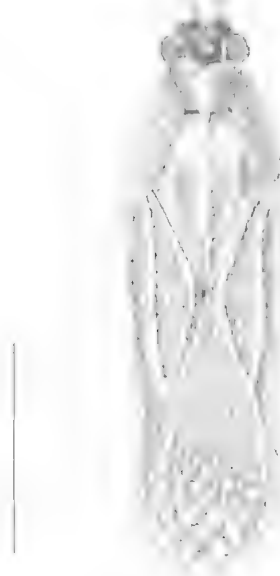
DESCRIPTION. Head, pronotum, legs and antennae beige to yellowish; abdomen dark brown; femora with a dark brown transverse medial band. Body long, with sparse minute pubescence, 2mm long, 0.74mm wide.

FIG. 2. *Leptoptyx varians* sp. nov., habitus.

Head small, with 5 slender, suberect, moderately long spines; occipital and median spines parallel; median and frontal spines slightly stouter than occipital spines; frontal spines crossed; antenniferous process short; bucculae broad, mostly triseriate, closed in front; labium reaching middle of mesosternum; labial channel moderately wide. Antennae long, slender, 1st and 2nd segments of equal length, I: 0.08, II: 0.08, III: 0.54, IV: 0.25; 4th segment slightly stouter, pilose. Legs short, slender; tarsi slender.

Pronotum gibbose, punctate; areolate on hind process, tricarinate; carinae subparallel, uniseriate; areolae tiny, indistinct; lateral carinae terminating anteriorly at calli; median carina slightly higher than lateral carinae, contiguous with collar; collar 4 areolae broad, erected medially as a tectiform hood higher than top of pronotum; hood extending back between calli to pronotal disc; paranota narrow, reflexed, resting on pronotum, 3 areolae broad; areolae subquadrate; 2 inner rows forming a ridge with last outer row, reaching median carinae anteriorly.

Hemelytra moderately broad and broadened at base, constricted in the middle, flat; costal area mostly biseriate, triseriate at widest part; subcostal area almost vertical, slightly sinuate, biseriate; discoidal area $> 1/2$ hemelytral length, 5

FIG. 3. *Leptoptyx longispina* sp. nov., habitus.

areolae broad; junction between RM and Cu at apex of discoidal area slightly tumid; sutural area broad at apex, 6 areolae broad; areolae larger than in other areas.

REMARKS. *L. varians* differs from *L. atopia* Drake & Ruhoff 1965 in having paranota 3 areolae broad and a discoidal area 5 areolae broad, while *L. atopia* has paranota 4 areolae broad and a discoidal area 7 to 8 areolae broad. *L. varians* differs from *L. icelia* Drake & Ruhoff 1965 by the costal area biseriate while it is uniseriate in *L. icelia*.

***Leptoptyx longispina* sp. nov.**
(Fig. 3)

HOLOTYPE. SOLOMON ISLANDS: ♂, Honiara, Guadalcanal, 0-200 m, xi.1980, NK. BPBM1981.79. PARATYPE: 1 ♀ same data as holotype, BPBM.

ETYMOLOGY. For the collector.

DESCRIPTION. Head dark brown; cephalic spines yellow; pronotum and hemelytra beige; hemelytra with some veinlets fuscous, legs and antennae beige; tarsi and first antennal segment slightly darker. Body long, narrow, glabrous. Body 2.4mm long, 0.71mm wide.

Head small, slightly pilose on top, with 5 long, slender spines; occipital and median spines

parallel, adpressed; frontal spines suberect, crossed; bucculae broad, biseriate; antennae long, slender, I: 0.12, II: 0.09, III: 0.79, IV: 0.37; 4th segment slightly stouter, more pilose; labium reaching middle of mesosternum; labial channel slightly enlarged posteriorly.

Pronotum narrow, long, gibbose, punctate, areolate on hind process, tricarinate; carinae distinctly uniseriate; areolae small; lateral carinae not reaching calli anteriorly but interrupted before top of pronotum; median carina higher than lateral carinae; collar 5 areolae broad, elevated medially as a tectiform hood extending backwards to pronotal disc; paranota reflexed, resting on the pronotum, almost touching base of lateral carinae, 4-5 areolae broad; 3-4 outer rows of areolae forming a ridge with the inner row.

Hemelytra long, narrow, flat, slightly constricted posteriorly at 2/3 length; costal area bent dorsally, narrow, uniseriate, areolae moderately large, subquadrate; subcostal area straight, bent downwards, narrow, biseriate, areolae small; discoidal area $>1/2$ hemelytra, 5 areolae broad at widest part, areolae small; junction of RM and Cu at apex of discoidal area slightly tumid; sutural area large at apex, 7 areolae broad at widest part, areolae small at base and large at apex.

REMARKS. *L. longispina* is easily distinguishable from *L. varians* by its narrower hemelytra and costal area, broader paranota and lateral carinae ending before the top of the pronotum. It differs from *L. atopia* which has a biseriate costal area and a sutural area 7-8 areolae wide. Very similar to *L. icelia*, it differs by its broader (4-5 areolae) paranota (2-3 in *L. icelia*), and longer cephalic spines. *L. atopia* and *L. icelia* have short cephalic spines while *L. varians* and *L. longispina* have long spines. The lateral carinae

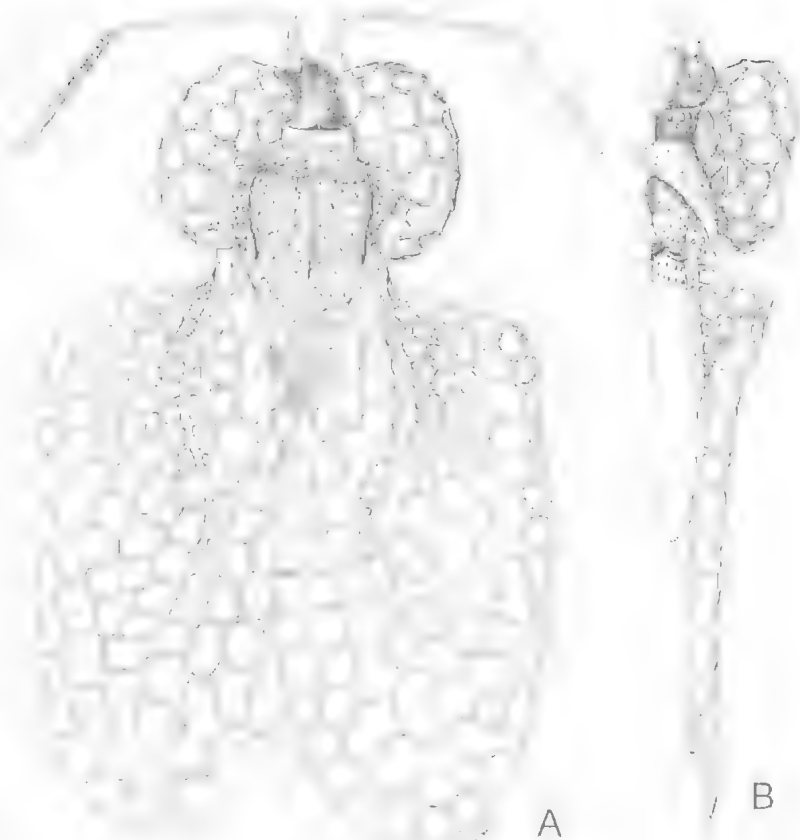


FIG. 4. *Nesocypsela strophii* sp. nov. A, habitus; B, profile.

of *L. atopia* are partly covered by the paranota unlike *variens*, *longispina* and *icelia*.

Nesocypsela Kirkaldy, 1908

Nesocypsela includes 12 species (including these 2 new species). Half are known from Fiji, and the others from neighbouring islands (Vanuatu, New Guinea, New Britain, New Ireland and now the Solomon Islands).

Nesocypsela strophii sp. nov.

(Fig. 4)

HOLOTYPE. SOLOMON ISLANDS: ♀ Popomanasiu, Guadalcanal, 4,400 m; 9-10.xi.1965, Hunuvalekama, Roy. Soc. Exped. Brit. Mus. 1966. 1, malaise trap, NIIM.

ETYMOLOGY. For the collector.

DESCRIPTION. Head, pronotum and abdomen dark brown. Hemelytra and paranota hyaline, veins beige to yellowish. Legs and antennae yellowish, except tarsi dark brown. Body length:

3.45, body width: 2.25, hood length: 0.83, hood width: 0.46.

Head small, sparsely pubescent, with 2 long, slender frontal spines. Bucculae small, short, mostly triseriate, slightly open in front. Labium long, reaching middle of metasternum. Labial channel broad, closed behind. Antenniferous process short, acute. Antennae long, slender, sparsely pubescent; I: 0.31, II: 0.11, III: 0.68, IV: 0.65. Legs long, slender; tarsi short, stout, pilose beneath.

Pronotum short, wide, tricarinate, slightly punctate, sparsely pilose; hind process rounded, not covering base of abdomen, with a transverse row of 6 rounded areolae on posterior margin. Carinae moderately narrow, raised, foliated, without areolae, extending from calli to posterior margin. Collar short, without hood, but anterior margin raised to form a small collarette. Paranota hyaline, large, reflexed but not resting on pronotum, outer margins not meeting dorsally but bent downwards, partly covering head but not covering pronotum, slightly serrate, 7 areolae wide, areolae large.

Hemelytra hyaline, much larger than abdomen, sharply widened at base. Outer margins anteriorly bent upwards, then bent downwards. Costal area wide, 6 areolae broad at widest part, areolae large. Subcostal area sinuate, bent downwards, uniseriate. Discoidal area small, biseriate, 7 areolae, inner areolae larger. Sutural area triseriate, areolae large.

REMARKS. *N. strophii* is distinguishable within the genus by its collarette and transverse row of areolae on the pronotum. It is very close to *N. muiri* Drake & Poor, 1943 (Fiji) which has a costal area 6 areolae deep, clouded black transverse bands on the hemelytra and 2 transverse rows of areolae on the posterior margin of the pronotum.

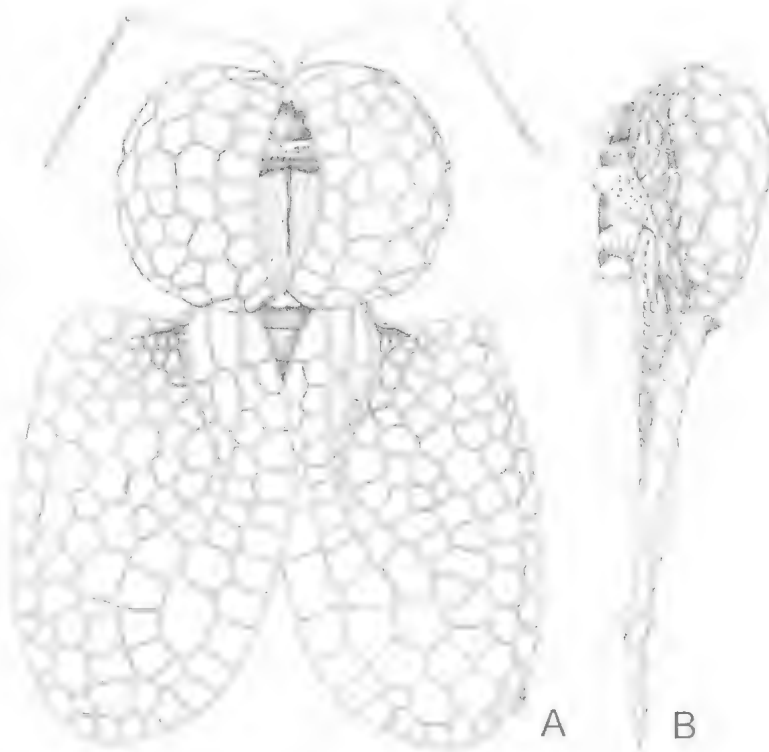


FIG. 5. *Nesocypsela simplex* sp. nov. A, habitus; B, profile.

***Nesocypsela simplex* sp. nov.**
(Fig. 5)

HOLOTYPE. SOLOMON ISLANDS: ♀ Popomanasiu, Guadalcanal, 4,400 m; 10.xi.1965, Hunuvalekama, Roy. Soc. Exped. Brit. Mus. 1966.1, low vegetation in camp, NHM.

ETYMOLOGY. For the collector.

DESCRIPTION. Head, pronotum and abdomen dark brown. Paranota hyaline, hemelytra hyaline, with slightly clouded spots, veins brown. Legs and antennae yellowish, except tarsi and 4th antennal segment dark brown. Body 4.84 long, 3.78 wide; hood 2.40 long, 1.75 wide.

Head small, spineless. Bucculae very small, short, biseriate, widely open in front. Labium reaching meso-metasternal suture. Labial channel broad, closed behind, ostiolar canal small. Antenniferous process short. Antennae long, slender, slightly pubescent; I: 0.35, II: 0.15, III: 1.23, IV: 0.92. Legs long, slender; tarsi short, stout, pilose beneath.

Pronotum short, wide, tricarinate, slightly punctate, sparsely pilose; hind process rounded,

not extending over base of abdomen, without areolae on posterior margin. Carinae moderately narrow, raised, foliate, without areolae, not reaching posterior margin. Collar short, without hood, triseriate. Paranota hyaline, large, raised, reflexed, not resting on pronotum, outer margins almost meeting in front and below but not meeting dorsally, partly covering head and pronotum, slightly serrate, 8 areolae wide, areolae moderately large.

Hemelytra hyaline, much larger than abdomen, sharply widened at base. Outer margins anteriorly bent upwards, then bent downwards. Costal area wide, 6 areolae broad at widest part, areolae large. Subcostal area sinuate, bent downwards, uniseriate, areolae larger than on costal area. Discoidal area small, barely distinct from the subcostal area, of 2 very large areolae. Sutural area biseriate, areolae large.

REMARKS. *N. simplex* resembles *N. evansi* Drake, 1953 generally, but differs in its non areolate posterior process of the pronotum and uniseriate subcostal area. It is distinguished within the genus by its paranota.

Nesocypselas dicysta Kirkaldy, 1908

NEW RECORDS. FIJI: ♂ Viti Levu: Nausori, II.1951, NK; 1 ♂ 2 sex undet., Rewa, Muir, XII.1905, BPBM.

REMARKS. *N. dicysta* is known only from Fiji.

Idiocysta China, 1930

Five of the 6 *Idiocysta* species are restricted to Fiji. *I. hackeri* is only known from Samoa.

Idiocysta vanuana sp. nov.
(Fig. 6)

HOLOTYPE. FIJI: ♀, Wainigata Res. Stn, Vanua Levu, 0-100m, S.X.1979, SL & GSS, BPBM1979.387.

DESCRIPTION. Head and body beneath black; pronotum, hemelytra, antennae and legs beige;

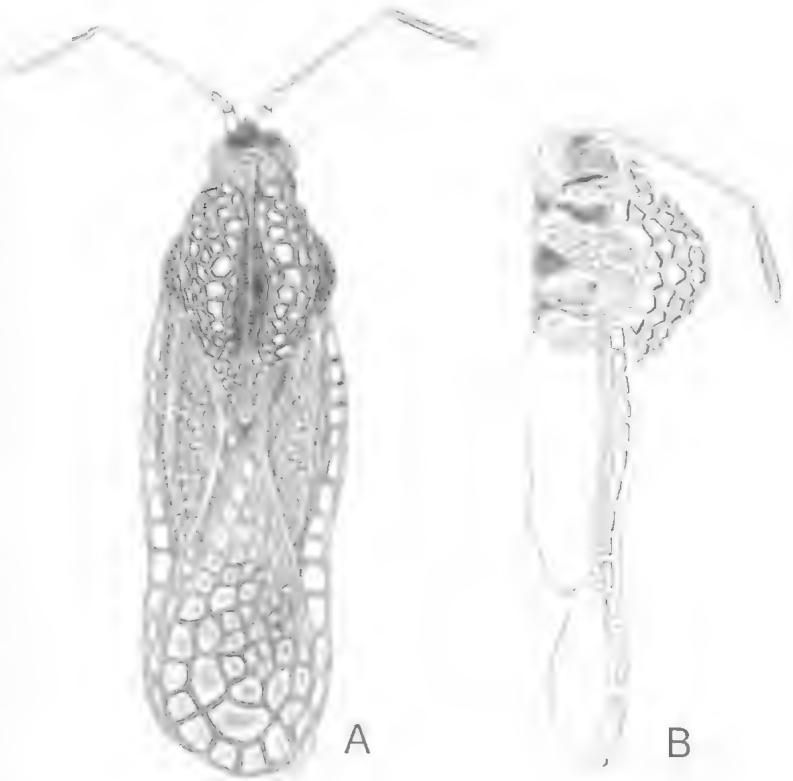


FIG. 6. *Idiocysta vanuana* sp. nov. A, habitus; B, profile.

posterior part of hemelytra and top of pronotum darker. Body 2.68 long, 0.89 wide.

Head small, short, armed with a short median spine; bucculae small, narrow, mostly triseriate, closed in front; labium almost extending beyond mesometasternal suture; labial channel widened and closed posteriorly; antennae long, slender, I: 0.12, II: 0.08, III: 0.55, IV: 0.43, 4th segment slightly pilose. Legs and tarsi long, slender.

Pronotum gibbose, punctate, areolate on hind process, tricarinate, densely pilose between carinae; carinae raised, uniseriate, areolae subquadrate, moderately large; collar narrow, biseriate, raised dorsally to form a tectiform hood, lower than median carina but higher than top of pronotum, slightly extending forwards but not covering head; paranota large, raised, reflexed but not resting on pronotum, not meeting dorsally, but covering part of pronotum, also covering lateral carinae but not median carina, 6 areolae wide; areolae deep, moderately large, polygonal.

Hemelytra narrow, a little wider than pronotum; principal veins slightly raised; costal area bent upwards, uniseriate, areolae large and

quadrate; subcostal area same width as costal area, straight, almost vertical, biseriate, areolae small and rounded; discoidal area narrow, $>1/2$ length of hemelytra, 4 areolae wide, areolae small and rounded; sutural area 5 areolae at widest part, areolae small anteriorly, large posteriorly.

REMARKS. *I. vanuana* is close to *I. bicolor* Drake & Poor, 1943 in hemelytral structure, however the paranota of *I. bicolor* are smaller (5 areolae wide) and meeting on top. It is also close to *I. dryadis* Drake & Poor, 1943 but its paranota are wider (6 areolae deep while *I. dryadis* 4). Its subcostal area is biseriate, while that of *I. dryadis* is bi- to triseriate. Also similar to *I. fijiana* Drake & Poor, 1943, it differs by its wider subcostal area (biseriate while that of *I. fijiana* is uni- to biseriate), and by its paranota (larger by one row of areolae) which do not meet dorsally.

***Idiocysta hackeri* China, 1930**

NEW RECORDS. SAMOA: 2♂, Upolu, Afiamalu, 8.VI.1940, 2200m, *Eugenia* sp., CH; 1♀, Upolu, Afiamalu, 24.VII.1940, 800m, beating, EZ; 1♀, Upolu, Afiamalu, 13.VII.1940, 1000m, beating dead branches, EZ. 1♀, Upolu, Malololei road, 8.VII.1940, 1600-1800m, beating shrubs, EZ. 1♀, Tutuila, 12.I.1958, WK, BPBM.

***Idiocysta fijiana* Drake & Poor, 1943**

NEW RECORDS. FIJI: 1♀, Viti Levu, Nukurua Forest, logged area, 60-130m, 15.X.1979. MK, GSS, BPBM 1979.260.

REMARKS. This specimen is slightly different from the type in that its paranota are almost closed dorsally but not as closed as in the type and the labium reaches the meso-metasternal suture, while in the type it extends to near the base of mesosternum.

***Idiocysta florid* Drake & Poor, 1943**

NEW RECORDS. FIJI: 2♂ 4♀, Viti Levu, Namosi Rd, 16 km N Queen's Hwy, 330m, 3-7.XI.1981, on *Alpinia boia* leaves, WG, BPBM 1981.601.

***Idiocysta dryadis* Drake & Poor, 1943**

NEW RECORDS. FIJI: 1♂, Viti Levu, Namosi Rd, 3km N Queen's Hwy, 100m, *Myristica* sp. leaves, BPBM 1981.601; 9♂ 3♀ 3 fifth instar larvae, Viti Levu, Foster's Pk, 10km N of Suva, 1100m, *Myristica* sp., BPBM 1981.601.

***Eteoneus* Distant, 1903**

Eteoneus comprises 20 species; 5 in the Ethiopian region, 1 in China; 14 in the Oriental



FIG. 7. *Eteoneus samoensis* sp. nov., habitus.

region from west India to the Bismarck Archipelago and Palau Islands. This is the first description of an *Eteoneus* species from Samoa and 2nd from Palau.

***Eteoneus samoensis* sp. nov.
(Fig. 7)**

HOLOTYPE.: AMERICAN SAMOA: ♀ Mulinu, Tutuila, 8.xii.1963, TM, BPBM.

DESCRIPTION. All body, antennae and legs brown fuscous. Body 4.39 long, 1.54 wide.

Head large, with sparse minute pubescence on top, armed with 4 spines; occipital spines short, slender; frontal spines small, tubercle-like; eyes very large, with post-ocular plate behind; bucculae small, narrow, triseriate, closed in front; labium long, reaching meso-metasternal suture; labial channel enlarged posteriorly, closed behind; 1st segment of antennae stouter than 2nd, I: 0.25, II: 0.15, 3rd and 4th segments lacking.

Pronotum strongly gibbose, long, clothed with short pubescence, deeply punctate, areolate on hind process, tricarinate; median carina distinct

all pronotum length; lateral carinae almost indistinct, present only on hind process, not reaching top of pronotum; calli wide, collar narrow, biseriate, not raised to form a hood; paranota almost indistinct, reduced to a slight ridge all pronotum length.

Hemelytra flat, not widened, same width as pronotum, covered with short pubescence; costal area straight, narrow, moderately bent upwards, uniseriate; areolae rounded, varying in size from small to moderately large; subcostal area narrow, slightly bent downwards, triseriate, areolae rounded and small; discoidal area $>1/2$ hemelytral length, 8 areolae wide at widest part, areolae small and rounded; sutural area large and short, 6 areolae wide at widest part, areolae small to large.

REMARKS. *E. samoensis* is easily distinguishable within the genus except for *E. sigillatus* Drake & Poor, 1936 by the uniseriate costal area. It differs from *E. sigillatus* in its lack of median cephalic spine.

***Eteoneus palauensis* sp. nov.**
(Fig. 8)

HOLOTYPE. PALAU: ♂, Imeliik Netkeng, Sabelthuap, 6.VI.1957, CS, BPBM.

DESCRIPTION. Head, pronotum, fuscous, hemelytra fuscous with a yellowish spot through costal and subcostal areas, at level of apex of discoidal area, body beneath brown; legs and antennae yellowish, except tarsi and 4th antennal segment brown. Body 2.62 long, 0.92 wide.

Head short, wide, slightly pilose on top, without spines; eyes large; bucculae short, broad, biseriate, closed in front; labium reaching meso-metasternal suture, labial channel wide, narrowed at apex, open behind; antenniferous process short; antennae long, slender, pilose; I: 0.14, II: 0.11, III: 0.94, IV: 0.54, 4th segment slightly stouter than others; legs slender, slightly pilose; tarsi long, slender, pilose.

Pronotum strongly gibbose, long, broad, punctate, clothed by short pubescence, unicarinate; carinae distinct, not raised all pronotum length; collar large, triseriate; paranota almost indistinct, reduced to a small ridge.

Hemelytra moderately longer and broader than body, the same width as pronotum, flat, constricted posteriorly at level of apex of discoidal area; costal area narrow, bent upwards, uniseriate, with areolae rounded and moderately large; subcostal area narrow, triseriate, with



FIG. 8. *Eteoneus palauensis* sp. nov., habitus.

areolae rounded and small; discoidal area $>1/2$ length of hemelytra, 5-6 areolae wide at widest part, areolae small, same size as subcostal area; sutural area wide, 7 areolae wide at widest part, areolae small to large posteriorly.

REMARKS. Like *E. samoensis*, *E. palauensis* differs from the other species by its uniseriate costal area. It differs from *E. samoensis* by lacking cephalic spines, smaller size and discoidal area 6-7 areolae wide. It differs from *E. sigillatus* by lacking cephalic spines and its triseriate subcostal area (pentaseriate in *E. sigillatus*).

***Eteoneus lectus* Drake, 1960**

NEW RECORDS. SOLOMON ISLANDS: 2♀, New Georgia, Gizo, 100m, 16.VII.1964, JS. 1♀, New Georgia, Munda, 0-200m, XI.1972, NK. 1♀, New Georgia, Munda, 0-100m, XI.1975, NK. 1♂, New Georgia, Munda, 0-100m, XI.1980, NK, BPBM1981.79. 1♀, New Georgia, Munda, 0-100m, XI.1976, NK, 1984-299, BPBM. 2♀ 2♂, Guadalcanal, Honiara, 0-200m, I.1984, NK, BPBM1984.168. 1♂ 2♀, Santa Ysabel, Kolotuve, 15.VI.1960, CO. 1♂, Kolombangara, Gizo, 0-140m, XII.1980, NK, BPBM1981.79.

REMARKS. This species is known from New Britain, Bismarck Archipelago, Philippines, NW New Guinea and the Solomon Islands.

***Eteoneus esakii* Drake, 1939**

NEW RECORDS. PALAU: 1♂, Malakal, 2.V.1957, CS. 6♂ 3♀, Koror, 19.IV.1957, sweeping *Premna* sp., CS, BPBM.

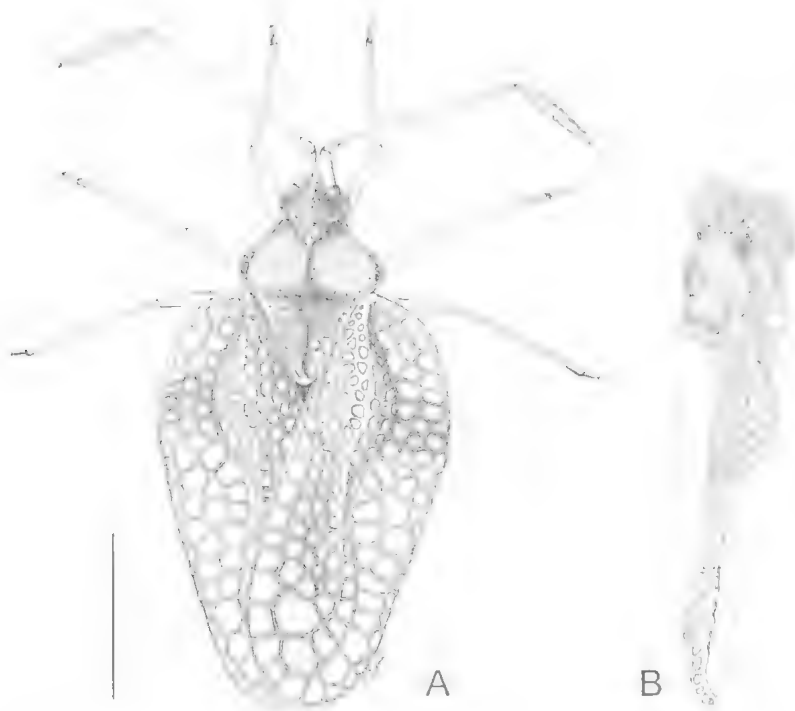


FIG. 9. *Omoplax majorcarinae* sp. nov. A, habitus; B, profile.

REMARKS. Known only from Palau Islands (Koror, Malakal, Peleliu).

Omoplax Horváth, 1912

Originally a subgenus of *Stephanitis*, was raised to full generic rank by Takeya (1962). It now contains two species from the same islands.

Omoplax majorcarinae sp. nov.
(Fig. 9)

HOLOTYPE. BONIN ISLANDS: ♂, Chuo san, Chichi Jima, 300 m, 23-25.VIII.1980, *Cinnamomum* sp., JG, BPBM1980.377. PARATYPES: all from Chuo san, Chichi Jima. 1 ♀, 300m, 23-25.VIII.1980, *Ligustrum* sp., JG, BPBM1980.377; 1 ♂, 300 m, 15.VIII.1980, JG, BPBM1980.377; 1 ♀, 300 m, 23-25.VIII.1980, JG, BPBM1980.377.

ETYMOLOGY. For the collector.

DESCRIPTION. Head, body, legs and antennae brown to yellowish; hemelytra with a dark spot on costal area at anterior third; body beneath darker. Body 3.45 long, 1.85 wide.

Head short, small, without cephalic spines; bucculae small, narrow, much narrower in front, mostly biseriate, closed in front; labium reaching middle of mesosternum; labial channel very

wide, wider and closed behind; antennae long, slender, I: 0.26, II: 0.12, III: 1.31, IV: 0.71, 4th segment slightly pilose.

Pronotum gibbose, punctate, areolate on hind process, unicarinate; carina all pronotum length, raised, uniseriate, with large areolae, subquadrate and hyaline, collar biseriate, inflated dorsally to form a hood cyst-like, narrow but sharply raised, extending forwards to cover part of the head, 4-5 areolae high, 8 areolae long, areolae small; paranota narrow, present all pronotum length, a small hyaline surface just near calli, ridge-like posteriorly, wider just opposite humeri, there raised, of 5-6 small areolae, outer margins slightly serrate.

Hemelytra sharply widened at base, wider at base than posteriorly, hyaline, with tumid area, outer margins slightly serrate, raised anteriorly and posteriorly bent downwards; costal area broad, 4-5 areolae broad at widest part, areolae large, angular; subcostal area wide anteriorly, narrow posteriorly, sinuate, 4 areolae wide at widest part, areolae small, tumid as to form a vesicle with discoidal area; discoidal area wide, tumid, 4 areolae wide at widest part, areola small; sutural area moderately wide, 3-4 areolae wide, areolae large, angular.

REMARKS. *Omoplax majorcarinae* is similar to *O. desecta*, and differs only in its labium extending to middle of mesosternum (beyond metasternum in *O. desecta*) and in its paranota having 5-6 (vs 3-5) areolae, and uniseriate median carina (vs biseriate).

Omoplax desecta Horváth, 1912
(Fig. 10)

NEW RECORDS. BONIN ISLANDS: 3 ♂ 5 ♀, Haha Jima, Okimura, 26.IV-9.VI.1958, FSr. 2 ♂, Chichi Jima, Sakai-ura, Bull beach, 12-31.V.1958 FS & WM. 1 ♀, Haha Jima, Chibusa Yama, 200-462 m, 17-20.VIII.1980, *Cinnamomum* sp., JG, BPBM1980.377. 2 ♂ 1 ♀, Haha Jima, Chibusa Yama, 200-462 m, 17-20.VIII.1980,

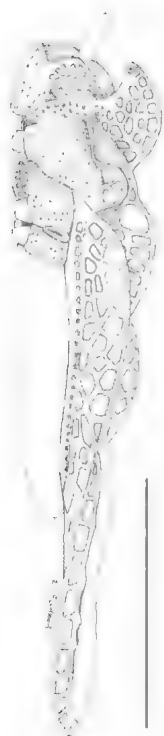


FIG. 10. *Omoplax desecta* Horváth, 1912, profile.

Terminalia sp., JG, BPBM1980.377. 1♂, Haha Jima, Chibusa Yama, 200-462 m, 17-20.VIII.1980, beating, JG, BPBM1980.377. 1♂ 2♀, Chichi Jima, Chuo san, 300 m, 23-25.VIII.1980, *Ligustrum* sp., JG, BPBM#1980.377. 1♀, Is., Chichi Jima, Chuo san, 300 m, 23-25.VIII.1980, *Cinnamomum* sp., JG, BPBM1980.377. 2♂ 1♀, Chichi Jima, Chuo san, 300 m, 23-25.VIII.1980, *Ardisia* sp., JG, BPBM1980.377. 1♀, Chichi Jima, Chuo san, 300m, 23-25.VIII.1980, JG, BPBM1980.377. 2♀, Chichi Jima, foot of Mt Shigure, 100 m, 16.VIII.1980, dead branches, JG, BPBM1980.377. 1♂ 2♀, Chichi Jima, 13-16.VIII.1980, host #3, JG, BPBM1980.377, BPBM.

REMARKS. *O. desecta* is known only from the Bonin Islands (Chichi Jima and Haha Jima).

Tingis Fabricius, 1803

Tingis parvoroe Guilbert, 1999

NEW RECORDS. SOLOMON ISLANDS: 1♀ 1♂, San Cristoval, Maniate, 6.VIII.1960, light trap, CO. 2♂, San Cristoval, Maniate, 5.VIII.1960, light trap, CO. 1♂, Guadalcanal, Roroni, 35km E of Honiara, 10m, 12.V.1964, light trap, RS. 1♀, Guadalcanal, Roroni, 35km E of Honiara, 10m, 9.V.1964, light trap, RS. 1♂, Santa Cruz, Graciosa Bay, 0-50m, I.1977, NK. 1♀, Mono, 150-300m, 6-11.XI.1980, *Bidens* sp., JG, BPBM1980.484. 1♀, New Georgia, Gizo, 30m, 13.VII.1964, light trap, JS. 1♀, San Cristoval, Wugiroga, 7.VIII.1960, light trap, CO, BPBM.

REMARKS. This species was described from Vanuatu, and is recorded for the first time from the Solomon Islands.

Perissonemia Drake & Poor, 1937

Perissonemia torquata Drake & Poor, 1937

NEW RECORDS. SOLOMON ISLANDS: 1♀ 1♂ 1 sex undet., Choiseul, Sasamongga, 0-100m, II.1984, NK, BPBM1984.168.

REMARKS. *P. torquata* is known from New Guinea, the Philippines and Solomon Islands. Minor differences exist between specimens from these localities. This species was described from Mindanao and has a labium reaching slightly beyond the middle of the metasternum, a triseriate subcostal area and paranota with 2 inner areolae opposite to calli. The outer row of areolae is tiny and without distinct veins on membranous margins. In addition, the outer row has 3 areolae, while some specimens from New Guinea (NMNH) are slightly different; the outer row of the paranota has >3 areolae with a minute outer vein; and the subcostal area is mostly biseriate. These specimens from the Solomons have the labium almost reaching the meso-metasternal suture, a triseriate subcostal area, and narrow paranota, with 1 row of small areolae and 2 extra inner areolae opposite the calli.

Eritingis Drake & Ruhoff, 1962

Eritingis includes 11 species; 9 from Australia (Qld, NSW and Sth Aust) and 2 from the Indo-Pacific region. The genus was erected for *Tingis*-like species with narrow paranota, uniseriate, erect and reflexed against the pronotum.

Eritingis recens (Drake & Poor, 1937)

NEW RECORDS. SOLOMON ISLANDS: 1♂, Guadal canal, Kukum, 18.X.1953. EB, N °3923, Press. By Com. Inst. Ent., B.M. 1958-79, NHM.

REMARKS. *E. recens* is known from Singapore, Vietnam, North Borneo, New Ireland and Palawan and now the Solomon Islands.

Eritingis pacifica (Kirkaldy, 1908)

NEW RECORDS. FIJI: 1♂ 1♀, Viti Levu, Korotongo, 0-100m, III.1981, NK, BPBM1981.131. 1♀, Viti Levu, Nandi, 0-50m, IV.1981, NK, BPBM1981.131.

REMARKS. Known from Fiji and New Britain.

Teleonemia Costa, 1864**Teleonemia scrupulosa Stål, 1873**

NEW RECORDS. FIJI: Viti Levu: Nandarivatu 850m-950m; Suva; Lami; 40km E of Nadi; Rakiraki 0-50m; Korotongo 0-100m; 90km E of Tavua; Tacirua. Ovalau: Levuka 0-200m. Vanua Levu: Nakawanga, Savusavu 0-100m. SOCIETY ISLANDS: Tahiti: Papeete 0-200m; Vallée de Papenoo 0-100m; Vaiufaua 500m; Punaauia 0-150m; Punaauia 0-50m; Fare Rau Ape-Aorai trail 600-1400m; Arue 90-150m. TONGA: Tongatapu: Nuku'alofa 0-100m; Kolovai 0-100m; Mu'a 0-100m; Houma 0-50m; Haamonga. Vavau: Neiafu 0-100m. Eua: Hafu 100-200m; Pangai 0-100m. SAMOA: Savaii: Salelologa 0-50m.

REMARKS. *T. scrupulosa* is a biocontrol species for *Lantana* sp. It is widely distributed in neotropical and oriental regions, also in the Indian islands and Australia. It occurs in Hawaii, Vanuatu, New Caledonia, Fiji, Tonga, Carolines, Solomon, Society Islands, Bismarck Archipelago and now Samoa.

Phatnoma Fieber, 1844**Phatnoma pacifica Kirkaldy, 1908**

NEW RECORDS. FIJI: 1♂, Vanua Levu, Nakawanga, 9.X.1955, JG. 1♂, Vanua Levu, trans-insular road above summit, 500-550m, 6-9.X.1979, dry forest, GSS, BPBM1979.387.

REMARKS. Known only from Fiji.

Holophygdon Kirkaldy, 1908

The genus contains only *H. melanesica* from Fiji and *H. nishidae* Guilbert (1999) from Vanuatu. It was included in the tribe Litadeini (Drake & Ruhoff, 1965), due to the greatly swollen and pilose 2nd tarsal segment, like *Litadea* China, 1924. However, both genera share many different character states with other genera. In addition, *Litadea* is monotypic and known only from Madagascar. A revision of these genera would probably not support the validity of this tribe.

Holophygdon melanesica Kirkaldy, 1908

NEW RECORDS. FIJI: 1♂, Viti Levu, Namosi, rd, 8km N Queen's Hwy, 320m, 3-7.XI.1981, MV light, BG & WG, BPBM1981.601. 1♂, Viti Levu, Namosi Rd, 14km N Queen's Hwy, 300m, 3-7.XI.1981, on climbing aroid, BG & WG, BPBM1981.601. 1♂, Viti Levu, Colo-i-suva, 3-6.III.1963, Malaise trap, CY. 1♂, Rewa, Muir, ? 1908. 1, Vanua Levu, Tabia (Thakaudrove), 0-2m, 5.X.1979, SL & GSS, BPBM 1979.387.

Berotingis Drake, 1956

Berotingis includes *B. yapensis* from Yap (Caroline Islands) and *B. guamensis* and *B. rugiana* from the Marianas (Guam and Rota, respectively). These last two species are the only Tingidae known from those islands. This genus was separated from *Tingis* (Drake, 1956) by the large eyes, narrow and scarcely reflexed paranota, absence of hood and the indistinct lateral carinae. It is allied to *Eteoneus* (*B. yapensis* was formerly included in this genus) by the large eyes, the wide paranota, and the indistinct lateral carinae.

Berotingis rugiana Drake, 1956

NEW RECORDS. MARIANAS: 7♂ 6♀, Rugi, Rota, 29.VI.1946. RO. BPBM925.

Stephanitis Stål, 1873**Stephanitis subfasciata Horváth, 1912**

NEW RECORDS. PALAU: 1♂, Angaur Is., 1.V.1954, *Hernandia* sp., JB, BPBM

REMARKS. This species is known from China, Taiwan, Java, Burma, India, New Guinea and Palau.

DISCUSSION

Species richness in the western Pacific varies greatly among the islands. Small islands are species poor, but endemism is high. The known tingid faunas of Hawaii, Tonga, and Society Islands are only *Teleonemia scrupulosa*, which is an introduced species. Excluding *T. scrupulosa*, the tingid fauna of Bonin, Marianas, and Samoa islands is represented by 2 endemic species each. 5 species are known from Palau, and 2 of them are endemic. Only 1 of 4 species known from the Carolines is endemic (to Yap); 10 species occur in Vanuatu, and 4 of them are endemic. New Caledonia has 14 species, all endemic; 20 of 21 species in Fiji are endemic, and 12 of the 21 species in the Solomons are endemic. Before 1999, only 2 species were known from Vanuatu, and 9 (including *T. scrupulosa*) were added to its fauna this year. A recent study of the New Caledonian fauna (Guilbert, in prep.) added 19 species (12 endemic). Thus that many species remain undiscovered on Pacific islands.

Many genera are restricted to the Pacific region. *Omoplax* has 2 species, both endemic to Bonin. *Nobarnus* Distant, 1920, including 5 species, is endemic to New Caledonia. *Nesocypselas* has 11 species distributed from Fiji

to New Guinea. *Leptotyph*, with 4 species, is known only from the Solomons and New Britain. The 7 species in *Idiocysta* are restricted to Fiji, Samoa and Vanuatu. *Holophygdon* has 1 species in the Solomons and 1 in Vanuatu. *Agaotingis* Montrouzier, 1861, *Cephalidiosus* (Guilbert, 1998) and *Corinthus* Distant, 1920, each with 2 species, are endemic to New Caledonia. *Berontingis* is restricted to the Carolines (Yap) and Marianas. However, high generic endemism in this region may be due to oversplitting at the generic level. Many monotypic endemic genera could be grouped with related genera. *Aulotingis* Drake & Poor, 1943, related to *Leptotypha* Stål, 1873, is monotypic and known only from Fiji. The long tubular hood-like lateral carinae separate it from *Leptotypha*. Monotypic, Fijian *Corythotingis* Drake & Poor, 1943, differs from *Physatocheila* Fieber, 1844 in its pronotal structure. Monotypic, Fijian *Nesocysta* Kirkaldy, 1908 is allied to *Nesocypselas* but differs in paranotal shape. Monotypic *Oeocharis* Drake & Ruhoff, 1965 from the Solomons, is distinguished by the globular hood concealing the pronotum.

ACKNOWLEDGEMENTS

I am grateful to Gordon Nishida, Bishop Museum, Hawaii, for the loan of specimens in his care, to Thomas J. Henry, National Museum of Natural History, Washington D.C. and Mike Webb, Natural History Museum, London, for access to collections. This study was supported in part by the Large Scale Facility, TMR program.

LITERATURE CITED

- CHINA, W. E. 1930. Heteroptera. In *Insects of Samoa and other Samoan terrestrial Arthropoda*, part II. Hemiptera, 3: 81-162. British Museum (Natural History).
- DISTANT, W.L. 1920. Rhynchota from New Caledonia. *Annals and Magazine of Natural History* series, 9, 6: 143-164.
- DRAKE, C.J. 1939. A new tingitid from Palau Islands (Hemiptera). *Mushi* 12: 102-103.
1941. New American Tingitidae (Hemiptera). *Journal of the Washington Academy of Sciences* 31: 141-145.
1946. A new tingid from Yap Island (Hemiptera). *Mushi* 17: 27-28.
1953. Synonymic data and description of new genera and species of Tingidae (Hemiptera). *Great Basin Naturalist* 13: 91-99.
1956. Hemiptera: Tingidae. In *Insects of Micronesia* vol. 7. Bernice P. Bishop Museum. Pp. 101-116.
1960. Tingidae of New Guinea. *Pacific Insects* 2: 339-380.
1965. Insects of Micronesia. Hemiptera: Tingidae. Occasional Paper of the Bernice P. Bishop Museum 7: 101-116.
- DRAKE, C.J. & POOR, M.E. 1936. New Indian Tingitidae (Hemiptera). *Indian Forest Records* 2: 141-149.
1937. Tingitidae from Malaysia and Madagascar (Hemiptera). *Philippine Journal of Sciences* 62: 1-18.
1943. Fijian Tingitidae (Hemiptera). Occasional Paper of the Bernice P. Bishop Museum 17: 191-205.
- DRAKE, C.J. & RUHOFF, F.A. 1962. Synonymic notes and descriptions of new Tingidae (Hemiptera). *Studia Entomologica* 5: 489-506.
1965. Lacebugs from New Guinea, Borneo, Solomons, and other islands of the Western Pacific and Indian oceans (Hemiptera: Tingidae). *Pacific Insects* 7: 243-290.
- FIEBER, F.X. 1844. *Entomologische Monographien*. Leipzig. 138 pp. Tingidae pp. 20-111.
- GUILBERT, E. 1997a. Two new species of *Dicysta* from New Caledonia (Hemiptera, Tingidae). *Zoosystema* 19 (2-3): 515-521.
- 1997b. Nouveaux Tingidae (Hemiptera) de Nouvelle-Calédonie. *Bulletin de la Société Entomologique de France* 102 (3): 293-298.
- 1998a. *Stenotrachelus*: a new genus and two new species of Tingidae (Hemiptera) from New Caledonia. *Australian Journal of Entomology* 37 (1): 17-21.
- 1998b. Revision of the New Caledonian genus *Nobarnus* (Hemiptera: Tingidae) with description of three new species. *European Journal of Entomology* 95: 395-406.
1999. Tingidae : Heteroptera) of Vanuatu (New Hebrides): new species and new records. *European Journal of Entomology* 96: 419-426.
- HACKER, H. 1928. New species and records of Australian Tingitoidea (Hemiptera). *Memoirs of the Queensland Museum* 9: 174-188.
- HORVATH, G. 1912. Species generis Tingitidarum *Stephanitis*. *Annales Musei Nationalis Hungarici* 10: 319-339.
1926. Hemipterologische Notizen aus Neiderländisch-Indien. *Treubia* 8: 327-330.
- KIRKALDY, G. W. 1908. A catalogue of the Hemiptera of Fiji. *Proceedings of the Linnean Society of New South Wales* 33: 345-391.
- MONTROUZIER, P. 1861. In Perroud & Montrouzier. *Essai sur la faune entomologique de Kanala (Nouvelle-Calédonie) et description de quelques espèces nouvelles ou peu connues*. *Annales de la Société Linnéenne de Lyon* 11: 46-256.
- STAL, C. 1873. *Enumeration Hemipterorum*, vol. 3. Kongliga Svenska Vetenskaps-Akademiens Förhandlingar 11: 1-163.
- TAKEYA, C. 1963. Taxonomic revision of the Tingidae of Japan, Korea, the Ryukyus and Formosa. *Mushi* 36: 41-75.

PARASITE FAUNA OF AUSTRALIAN MARINE OLIGOCHAETES

SASCHA L. HALLETT, CHRISTER ERSÉUS, PETER J. O'DONOGHUE
AND ROBERT J.G. LESTER

Hallett, S.L., Erséus, C., O'Donoghue, P.J. & Lester, R.J.G. 2001 06 30: Parasite fauna of Australian marine oligochaetes. *Memoirs of the Queensland Museum* 46(2): 555-576. Brisbane. ISSN 0079-8835.

A survey of 7,200 marine oligochaetes from Queensland (Moreton Bay, Brisbane, Heron Island and Lizard Island), New South Wales (Georges River, Sydney) and the Northern Territory (Darwin Harbour) revealed infections by 5 major parasite groups. Tubificid oligochaetes of the Limnodriloidinae, Phallodrilinae and Rhyacodrilinae were host to: 10 actinosporeans (Myxozoa) namely *Sphaeractinomyxon ersei*, *S. leptocapsula*, *Endocapsa rosulata*, *E. stepheni*, *Endocapsa* type 1 nov., *Tetraspora discoidea*, *T. rotundum*, *Triactinomyxon* of Roubal et al., 1997, *Triactinomyxon* type 1 nov. and *Triactinomyxon* type 2 nov.; an aseptate eugregarine (Apicomplexa) *Oligochaetocystis* sp.; an astomate ciliate (Ciliophora); a peritrichous ciliate *Scyphidia* sp. (Ciliophora); mermithid nematodes (Nematoda); a haplosporidian (Haplosporidia); and a coccidian (Apicomplexa). A single encyrtid specimen, *Grania* sp., harboured astomate ciliates. □ *Australia, actinosporeans, marine oligochaetes, parasites, protozoans.*

Sascha L. Hallett (sascha@wildfire.com.au), Peter J. O'Donoghue & Robert J.G. Lester, Department of Microbiology and Parasitology, The University of Queensland, St Lucia, Queensland 4072, Australia; Christer Erséus, Department of Invertebrate Zoology, Swedish Museum of Natural History, Box 50007, SE-104 05 Stockholm, Sweden; 22 September 2000.

The literature suggests that parasites of marine oligochaetes are common (Giere & Pfannkuche, 1982; Raftos & Cooper, 1990), yet few specific examples can be found. Documented parasites belong principally to the protozoan orders Astomata (Ciliophora: Holotricha) and Gregarinida (Apicomplexa: Telosporidia) with at least 13 and 5 species described, respectively (Giere & Pfannkuche, 1982). Six actinosporeans (Myxozoa), *Sphaeractinomyxon stolci* Caullery & Mesnil, 1904, *Sphaeractinomyxon* type 1 & 2 Hallett et al., 1997a and *Aurantiaactinomyxon* type 1, 2 & 3 Hallett et al., 1997a, also have been recorded. Prior to this study, no parasites had been recorded from an Australian marine oligochaete.

Freshwater oligochaetes are reported as hosts to these parasite groups as well as to cestodes (e.g. *Archigetes iowensis* and *Hunterella nodulosa*), nematodes (e.g. *Eustrongylides* sp., *Diectophyma renale*) (Raftos & Cooper, 1990) and rotifers *Albertia* spp. (Koste, 1970; Erséus, 1976). They also are host to about 116 actinosporeans (McGeorge et al., 1997; Lom et al., 1997; Xiao & Dessler, 1998a, b; El-Mansy et al., 1998b,c); some of these parasites are alternate stages in the life cycles of myxosporeans (Myxozoa) in fish (see Kent et al., 1994a; Lom et al., 1997). To date, some 24 life cycles have been elucidated and they have all involved freshwater

species for which no other form of life cycle is known. No complete life cycle has been determined for any marine myxozoan. Myxosporeans are common in marine fish in Australia; this study was undertaken to determine if actinosporeans were present in Australian marine oligochaetes. Some of our early findings have been published elsewhere. These records are of the actinosporeans *Sphaeractinomyxon ersei* Hallett, O'Donoghue & Lester, 1998, *S. leptocapsula* Hallett, Erséus & Lester, 1999, *Endocapsa rosulata* Hallett, Erséus & Lester, 1999, *E. stepheni* Hallett, Erséus & Lester, 1999, *Tetraspora discoidea* Hallett & Lester, 1999, *T. rotundum* Hallett & Lester, 1999, and *Triactinomyxon* of Roubal et al., 1997. Here, we present a review of all parasite types so far encountered in Australian marine oligochaetes, including published records.

MATERIALS AND METHODS

Sediment samples were collected to a depth of 15cm from the intertidal zone in Moreton Bay (27°15'-25°S), and from Heron (23°27'S, 151°55'E) and Lizard (14°40'S, 145°28'E) Islands during 1995-1997 (Fig. 1). Infected oligochaetes were also obtained from Sydney, NSW (33°53'S, 151°10'E) and Darwin, NT (12°25'S, 130°51'E) (Fig. 1B). Sediment was collected in 500ml jars, each emptied into a

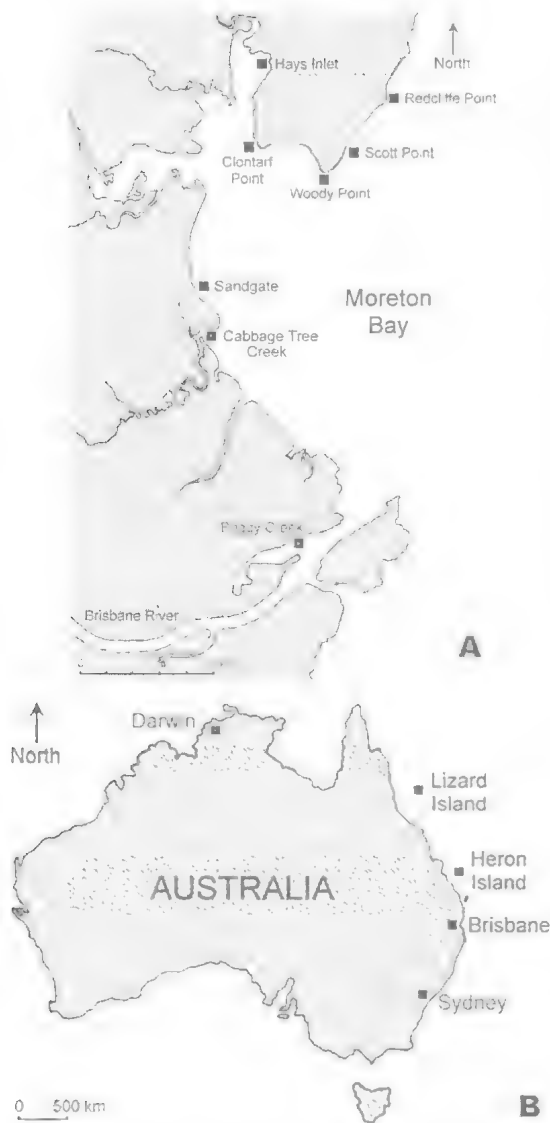


FIG. 1. A, Moreton Bay collecting localities. B, Map of Australia showing other collecting localities. Brisbane incorporates Moreton Bay.

bucket containing about 4 litres of seawater, thoroughly mixed and the supernatant poured through a 0.4mm sieve. The contents of the sieve were washed into a petri dish and the supernatant returned to the bucket. This process was repeated about 5 times per sample. The material in the petri dish was then examined under a dissection microscope and any oligochaetes present were recovered for detailed examination under a compound microscope. The worms were placed on glass slides and a drop of 25% ethanol in

seawater was added to inhibit movement. Parasites (with the exception of those obtained from Lizard Island, Darwin Harbour and Sydney) were photographed, sketched and measured prior to fixation in either Bouin's fixative for 24 hours for host identification or 3% glutaraldehyde in 0.066M cacodylate buffer for 24 hours for electron microscopy. For host identification, infected oligochaetes were transferred to 70% ethanol, stained in alcoholic paracarmine, mounted whole in Canada Balsam and examined under a compound microscope. Nematodes were fixed within the oligochaete host and several were cleared and stained with chlorolactophenol and Mayer's haematoxylin. Actinosporean descriptions follow the guidelines presented by Lom et al. (1997) except that 'germ cell' is used for 'daughter cells' and we give an additional measurement 'basal width' which is maximum width of the spore in apical view. New forms are identified in accordance with Kent et al. (1994) and Lom et al. (1997). Reference oligochaete host specimens containing parasites are lodged in the Queensland Museum (QM), Brisbane.

RESULTS

A total of 5,200 oligochaetes were examined from Moreton Bay and a further 2,000 oligochaetes from Heron Island. The density of worms sampled in Brisbane was up to 0.8 worms per cm³. Six parasitic/commensal groups were identified: actinosporeans (Myxozoa), aseptate eugregarines (Apicomplexa), astomate and peritrichous ciliates (Ciliophora), mermithid nematodes (Nematoda), haplosporidians (Haplosporidia) and coccidians (Apicomplexa) (Tables 1, 2).

Phylum MYXOZOA Grassé, 1970

Class MYXOSPOREA Bütschli, 1881

ACTINOSPOREAN FORMS Kent et al., 1994

Infections by actinosporeans were detected in 196 (3.8%) of 5,200 worms from Moreton Bay, 25 (1.3%) of 2,000 worms from Heron Is. and in 8 worms from Lizard Is. One worm from Moreton Bay harboured a double infection of *Sphaeractinomyxon ersei* and *Tetrastora discoidea*. Three worms, *Duridrilus* sp. (QMG463613), *Limnodriloides* sp. (QMG463615) and *Doliodrilus diverticulatus* (QMG463614) from Darwin Harbour and an unidentified oligochaete from Georges River, Sydney, harboured unidentified actinosporeans (all fixed samples). Ten actinosporeans belonging to 4 collective groups were found in marine oligochaetes (Table 1).

TABLE 1. Actinosporeans from Australian marine oligochaetes.

Actinosporean	No. Infected Hosts	Host	Site
<i>Sphaeractinomyxon ersei</i>	2	<i>Doliodrilus diverticulatus</i>	Moreton Bay
	1	<i>Limnodriloides cf. victoriensis</i>	Moreton Bay
	44	Tubificidae sp./spp.	Moreton Bay
	2	Tubificidae sp./spp.	Heron Island
	1	<i>Thalassodriloides cf. gurvitschi</i>	Lizard Island
	2	<i>Limnodriloides lateroporus</i>	Lizard Island
	1	<i>Bathydrilus</i> sp.	Lizard Island
<i>Sphaeractinomyxon</i> spp.	24	Tubificidae sp./spp.	Moreton Bay
<i>S. leptocapsula</i>	2	<i>Heronidrilus</i> sp.	Lizard Island
<i>Endocapsa rosulata</i>	3	<i>Heterodrilus cf. keenani</i>	Heron Island
	1	<i>Thalassodriloides cf. gurvitschi</i>	Lizard Island
	1	<i>Heronidrilus</i> sp.	Lizard Island
<i>E. cf. rosulata</i>	9	Tubificidae sp./spp.	Moreton Bay
	6	Tubificidae sp./spp.	Heron Island
<i>E. stepheni</i>	1	<i>Heterodrilus cf. keenani</i>	Heron Island
	2	<i>Heterodrilus queenslandicus</i>	Heron Island
	1	Tubificidae sp.	Heron Island
<i>Endocapsa</i> type 1	8	Tubificidae spp.	Moreton Bay
<i>Tetraspora discoidea</i>	2	<i>Doliodrilus diverticulatus</i>	Moreton Bay
	12	Tubificidae sp./spp.	Moreton Bay
<i>Tetraspora rotundum</i>	3	Tubificidae sp./spp.	Moreton Bay
<i>Triactinomyxon</i> sp.	1	<i>Limnodriloides cf. victoriensis</i>	Moreton Bay
	24	Tubificidae sp./spp.	Moreton Bay
<i>Triactinomyxon</i> type 1	1	<i>Limnodriloidinae</i> sp.	Moreton Bay
<i>Triactinomyxon</i> type 2	1	Tubificidae sp.	Moreton Bay
Unidentified:			
<i>Sphaeractinomyxid</i>	10	Tubificidae sp./spp.	Heron Island
coelomic infection	53	Tubificidae sp./spp.	Moreton Bay
intestinal infection	12	Tubificidae sp./spp.	Moreton Bay
coelomic infection	1	<i>Duridrilus</i> sp.	Darwin Harbour
coelomic infection	1	<i>Limnodriloides</i> sp.	Darwin Harbour
coelomic infection	1	<i>Doliodrilus diverticulatus</i>	Darwin Harbour
infection	1	Tubificidae sp.	Sydney

SPHAERACTINOMYXON FORMS

***Sphaeractinomyxon ersei* Hallett,
O'Donoghue & Lester, 1998
(Fig. 2A)**

TYPE HOST. *Doliodrilus diverticulatus* Erséus, 1985 (Tubificidae: Limnodriloidinae).

SITE IN HOST. Immature stages located within the coelom and mature spores present in the intestinal lumen.

TYPE LOCALITY. Boggy Creek, Moreton Bay, 27°24'S, 153°09'E.

SPECIMENS LODGED. QM G462452 (#110), G462453 (#185), G462465 (#210), G463601 (LI95-4), G463602 (LI95-24/1), G463603 (LI95-24a), G463604 (LI95-24b).

DESCRIPTION. Triradially symmetrical spores packed in groups of eight in the pansporocyst. Spores triangular in apical view, diameter 17-34µm, basal width 17-33µm; ellipsoidal in side view, length 17-33µm. Polar capsules, 3, round to pyriform, centrally located, diameter

(width) 3-5.5µm, length 3-7µm. Sporoplasm, rounded triangular in apical view, single binucleate, about 46 germ cells, almost fills the spore cavity.

REMARKS. *S. ersei* was detected in 47 (0.9%) of 5,200 oligochaetes examined from Moreton Bay; the number may be higher because 77 unidentified (immature) coelomic actinosporeans were also recorded (see Table 1). It also infected *Limnodriloides cf. victoriensis* Brinkhurst & Baker, 1979 from Boggy Creek, tubificid species from Heron Is. and *Thalassodriloides cf. gurvitschi* (Hrabe, 1971) (Limnodriloidinae), *Limnodriloides lateroporus* Erséus, 1997 and *Bathydrilus* sp. (immature) (Tubificidae: Phallodrilinae) from Lizard Is.

***Sphaeractinomyxon leptocapsula*
Hallett, Erséus & Lester, 1999
(Fig. 2B)**

TYPE HOST. *Heronidrilus* sp. (2 immature specimens infected) (Tubificidae: Rhyacodrilinae).

TABLE 2. Parasites and commensals identified from Australian marine oligochaetes. #NR = not recorded.

Parasite	No. Infected Hosts	Host	Site
APICOMPLEXA <i>Oligochaetocystis</i> sp. Unidentified coccidian species	1 NR	Tubificidae sp. Limnodriloidinae sp./spp.	Moreton Bay Moreton Bay
CILIOPHORA <i>Radiophrya</i> sp. Unidentified astome <i>Scyphidia</i> sp.	43+ 1 NR	Tubificidae spp. <i>Grania</i> sp. Limnodriloidinae sp./spp.	Heron Island Heron Island Moreton Bay
HAPLOSPORIDIA <i>Haplosporidium</i> sp.	1 15	<i>Heterodrilus</i> sp. Tubificidae sp./spp.	Heron Island Heron Island
NEMATODA Mermithid nematode	1 4	<i>Heterodrilus</i> cf. <i>keenani</i> Tubificidae sp./spp.	Heron Island Heron Island

SITE IN HOST. Coelom.

TYPE LOCALITY. Intertidal sand, Lizard Is., 14°40'S, 145°28'E.

SPECIMENS LODGED. QMG462459 (LI95-16b), G462460 (LI95-16e).

DESCRIPTION. Spores triangular in apical view, diameter 20-24µm, basal width 20-23µm, length 17-22µm. Outer valve cell membrane follows contours of inner valve cell membrane. Polar capsules ~5µm long, slender, pyriform, orientated with pointed ends facing centre of spore, each positioned opposite a corner of spore about midway along spore radius, each contain polar filament with at least two turns. In side view, spore ellipsoidal to broad pyriform. Suture lines not discernible. Pansporocysts each with eight spores.

REMARKS. *S. leptocapsula* was observed on only in 2 oligochaetes from Lizard Is.

ENDOCAPSA FORMS

Endocapsa rosulata

Hallett, Erséus & Lester, 1999
(Fig. 2C-F)

TYPE HOST. *Heterodrilus* cf. *keenani* Erséus, 1981 (Tubificidae: Rhyacodrilinae).

SITE IN HOST. Immature stages in coelom; mature spores in intestinal lumen (Fig. 2E-F).

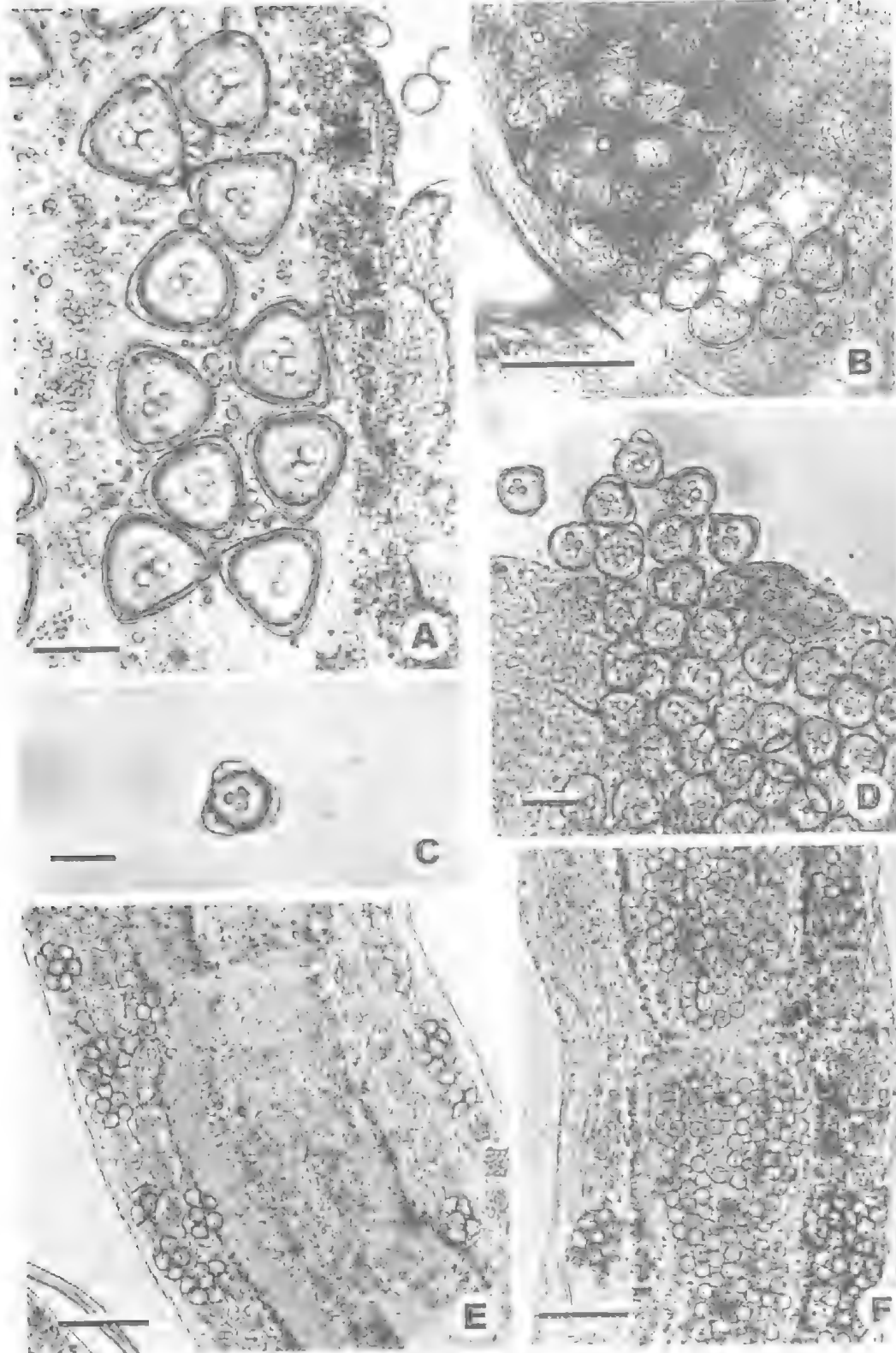
TYPE LOCALITY. Heron Is., 23°27'S, 151°55'E.

SPECIMENS LODGED. QM G462454 (H122), G462455 (H146), G463605 (LI95-24c), G463606 (LI95-16a), G462723 (#200).

DESCRIPTION. Spore diameter 25-27µm, basal width 25-28µm, length 20-23µm, resembles rosette in apical view, compressed dorsoventrally in side view (Fig. 2C); develops in groups of 8 within pansporocysts (55-75µm). Valve cells inner membrane subspherical; outer membrane follows contours of dorsal and ventral surfaces of this but exhibits swellings laterally in 3 regions equidistantly apart; inner and outer membranes close at each valve junction; suture lines prominent. Valve cell swellings formed within host, little or no further expansion on contact with seawater (Fig. 2D). Cavity diameter 19-23µm, ellipsoidal in side view. Polar capsules ellipsoidal, 4-5µm long and wide, located beneath a suture line anteriorly in, but not extruding from, spore, adjacent to remains of capsulogenic cell and perpendicular to processes, embedded in sporoplasm in side view, with polar filament with at least 3 turns. Sporoplasm granular, remaining areas of spore clear.

REMARKS. *Thalassodrilides* cf. *gurwitschi* and *Heronidrilus* sp. (immature) from Lizard Is. and tubificids from Moreton Bay also harboured this parasite. Nine tubificids of the 5,200 oligochaetes from Boggy Creek, Moreton Bay, were infected. Spores were observed only in the coelom; none were found in the gut lumen as were Heron Is. infections. Spores were smaller

FIG. 2. Actinosporians from marine oligochaetes. A, mature *Sphaeractinomyxon ersei* spores (each with 3 polar capsules) in the intestinal lumen of a limnodriloidine oligochaete from Moreton Bay. Fresh, unstained material. Scale = 25µm; B, *Sphaeractinomyxon leptocapsula* pansporocysts with eight spores in the coelom of an oligochaete. Preserved material from Lizard Island. Scale = 50µm. C-F, *Endocapsa rosulata*, fresh unstained material. C, Moreton Bay; D-F, Heron Island. C, spore in sea water. Scale = 20µm; D, spores emerging from host. Scale = 25µm; E, developing stages of *E. cf. rosulata* in coelom. Scale = 150µm; F, spores of *E. cf. rosulata* free in intestinal lumen. Scale = 150µm.



than those from Heron Is. being 20-25µm in diameter and 25-28µm in basal width.

Endocapsa stepheni Hallett, Erséus
& Lester, 1999

TYPE HOST. *Heterodrilus* cf. *keenani*.

SITE IN HOST. Coelom.

TYPE LOCALITY. Heron Is., 23°27'S, 151°55'E.

SPECIMENS LODGED. QM G462456 (H132), G462457 (H135), G462458 (H148).

DESCRIPTION. Spore, diameter 25-28µm, basal width 23-25µm, length ~20µm, irregularly shaped in apical view. Spore cavity diameter ~23µm. Valve cells follow shape of roughly triangular spore cavity but with a single lobe-like swelling at one corner. Sutures, detectable, from corners to middle of spore. Sporoplasm roughly triangular in apical view, almost fills spore cavity, depressed in side view where polar capsules positioned. Polar capsules round in apical view, diameter 4-5µm, pyriform in side view, length 4-5µm, centrally located in spore, close to each other, beneath suture lines. Spore appearing ellipsoidal in side view, except that valve cells form an extension at one side.

REMARKS. One *Heterodrilus* cf. *keenani*, 2 *H. queenslandicus* Jamieson, 1997 and 1 unidentified tubificid were infected with this actinosporean.

Endocapsa type 1 nov.
(Fig. 3)

HOST. Immature tubificids.

SITE IN HOST. Developing stages in peritoneum, mature spores in coelom and intestinal lumen.

LOCALITIES. Hays Inlet and Boggy Creek, Moreton Bay, 27°16'S, 153°04'E and 27°24'S, 153°09'E.

DESCRIPTION. Spores subtriangular in apical view, diameter 17-30µm (22µm, n=8), basal width 19-31µm (25µm, n=2) (Fig. 3A). Spore body (inner valve cell membrane) basically round but corner formed at 3-way valve junction (Fig. 3A, C). Valve cells, upon contact with sea water, form 3 equally-sized biconcave processes (swellings) which join at their narrowest part at each 3-way valve junction (Fig. 3A, C). Swellings frequently present prior to spore contact with seawater. Polar capsules round, oval to pyriform in side view, diameter 3-5µm (4µm, n=4), located centrally in spore, proximal to one

other, each situated beneath a suture (and therefore opposite a spore corner) (Fig. 3A), embedded in anterior part of sporoplasm, do not form an apex (Fig. 3B). Spore round in side view, length 16-28µm (22µm, n=7), diameter 19-31µm (25µm, n=6) (Fig. 3B).

REMARKS. Some spores had smooth rather than pinched corners. The non-protrusive polar capsules and reduced swellings, at times present within the host, place this actinosporean in the *Endocapsa*. Two other forms of *Endocapsa* have been recorded: *E. rosulata*; and *E. stepheni*. *Endocapsa* type 1 differs from both these in the shape of the spore and swellings. Its valve swellings encompass fully the spore body (visible in both apical and side view), whereas those of *E. rosulata* do not, and it possesses 3 swellings whereas *E. stepheni* forms just one. The Aurantiactinomyxon types described from Hong Kong marine oligochaetes possess valve projections rather than swellings and the spores are considerably smaller, being less than 20µm (Hallett et al., 1997). The principal difference between the Neoactinomyxon types described by El-Mansy et al. (1998b) and *Endocapsa* type 1 is that the valve cells of the former form triangular shaped extensions whereas they are curved in the valve cells of the latter. *Endocapsa* type 1 was recorded from 8 tubificid specimens.

TETRASPORA FORMS

Tetraspora discoidea Hallett & Lester, 1999
(Fig. 4A)

TYPE HOST. *Doliodrilus diverticulatus* Erséus, 1985 (Tubificidae: Limnodriloidinae).

SITE IN HOST. Coelom.

TYPE LOCALITY. Boggy Creek, Moreton Bay, 27°24'S, 153°09'E.

SPECIMENS LODGED. QM G462461 (#104), G462462 (#114), G462463 (#96).

DESCRIPTION. Spore diameter 33-52µm, basal width 33-38µm, length 14-22µm, disc-like, almost round, valve junctions form corner in apical view, dorsoventrally compressed in side view. Valve cell processes absent. Polar capsules, 3, subspherical in apical view, each within a pyriform capsulogenic cell, situated beneath a spore suture line, opposite a spore corner, bases proximal; pyriform in side view, located midway across spore at dorsal surface of sporoplasm. Polar filament oblique, at least 7 turns. Sporoplasm, shape similar to spore, unisporeal,

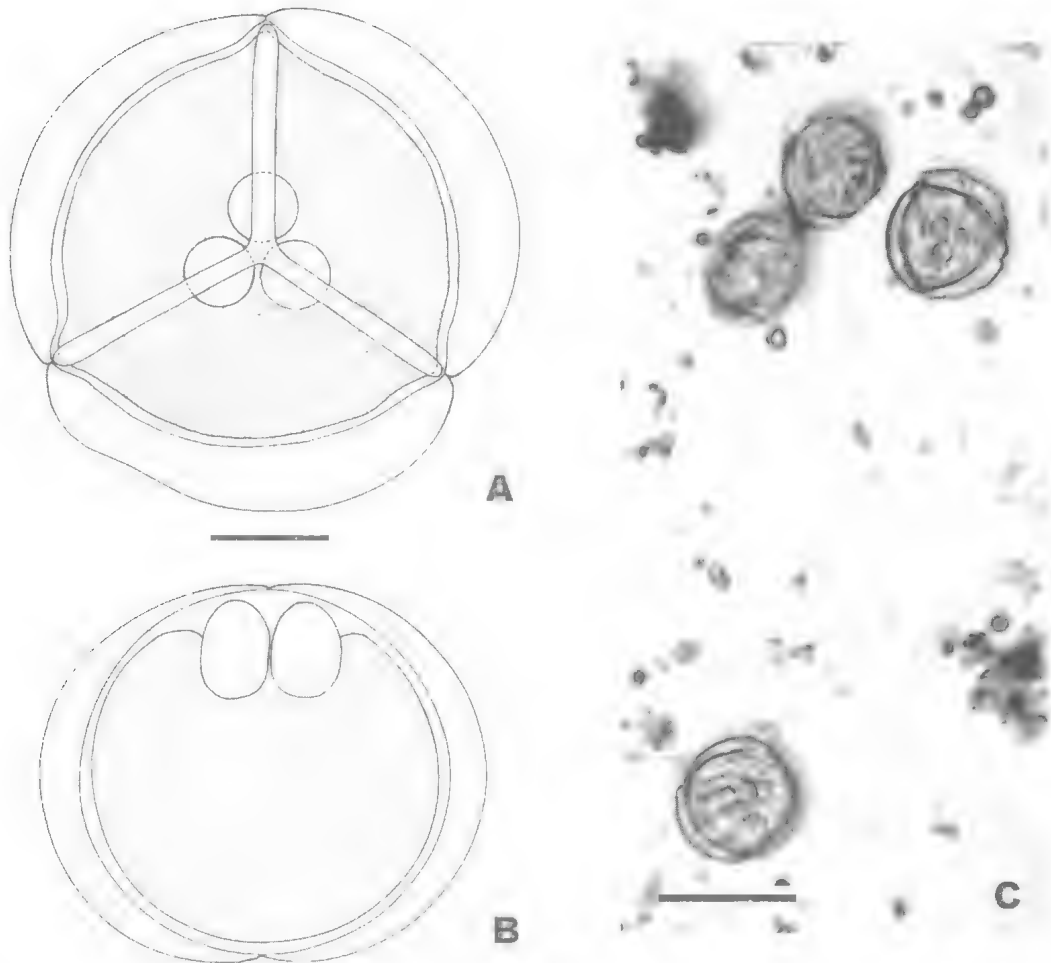


FIG. 3. *Endocapsa* type 1 nov. from fresh material from Moreton Bay. A, drawing of apical view and B, side view. Scale = 5µm. C, spores in seawater. Scale = 50µm.

contains at least one somatic nucleus and >100 germ cells. Pansporocysts, freely floating within host coelom, irregularly shaped, 47-70µm, each containing 4 developing spores. Spores do not alter in size or shape following release from host. Development between pansporocysts asynchronous, but within synchronous.

REMARKS. Twelve immature unidentifiable Tubificidae from Boggy Creek and 2 specimens of *D. diverticulatus* from Hays Inlet were infected with this parasite.

Tetraspora rotundum Hallett & Lester, 1999
(Fig. 4B)

TYPE HOST. Immature Tubificidae sp.

SITE IN HOST. Coelom.

TYPE LOCALITY. Boggy Creek, Moreton Bay, 27°24'S, 153°09'E.

SPECIMENS LODGED. QM G462464 (#113, #186).

DESCRIPTION. Triradially symmetrical spores packed in groups of eight in the pansporocyst. Spores triangular in apical view, diameter 17-34µm, basal width 17-33µm; ellipsoidal in side view, length 17-33µm. Polar capsules, three, round to pyriform, centrally located, diameter (width) 3-5.5µm, length 3-7µm. Sporoplasm, rounded triangular in apical view, single binucleate, about 46 germ cells, almost fills the spore cavity.

REMARKS. Three tubificids from Boggy Creek harboured *T. rotundum*.



FIG. 4. *Tetraspora* spores; fresh unstained material. A, *T. discoidea* in seawater. Scale = 10 μm. B, *T. rotundum* pansporocysts (arrows) with four spores. Scale = 20 μm.

TRIACTINOMYXON FORMS

Triactinomyxon of Roubal et al., 1997 (Figs 5, 6)

HOST. *Limnodriloides* cf. *victoriensis*.

SITE IN HOST. Immature stages in intestinal epithelium (Fig. 6B, D) and mature spores present also in intestinal lumen.

LOCALITIES. Hays Inlet, Clontarf Point, and Boggy Creek, Moreton Bay, 27°15–25'S

DESCRIPTION (expanded from Roubal et al., 1997). Spore anchor-shaped, total length 96–142 μm (125 μm, n=6) (Fig. 5A). Valve cells inflate upon contact with seawater to form 3 anteriorly curved projections (caudal processes) from spore stylus at 90–100° angle (α) (Figs. 5A, 6A). Projections equal length 94–185 μm (138 μm, n=6) and width, at end taper to a point, equidistantly apart, arm base not wider than stylus base. Polar capsules, three, 3–5 μm (4 μm, n=5) long, located at anterior end of stylus,

pyriform, protrude at apex, bases abut, anterior end of each at slight angle (c.45°) facing away from other polar capsules (Fig. 5 inset). Stylus widens gradually from tip to base (to ~22 μm). Sporoplasm, single, 17 μm long, with indiscernible number of germ cells, irregularly in the stylus.

REMARKS. This Triactinomyxon most closely resembles *T. legeri* Mackinnon & Adam, 1924 and *T. ignotum* Stolc, 1899, but spore dimensions are most like *T. legeri* (style 90–140 μm, arms 150 μm, sporoplasm 15–20 μm [Marques, 1984]). *T. legeri* and *T. ignotum* differ in size and number of germ cells in the sporoplasm (*T. legeri* = 24; *T. ignotum* = 8) and both develop in the intestinal epithelium of *Tubifex* freshwater oligochaetes. Triactinomyxon differs from *T. legeri* in its host and environment but these characters are considered insufficient to establish a new species. The number of germ cells was indeterminable by light microscopy in the marine triactinomyxon but the size of the sporoplasm suggests about 32. The orientation of the processes varied between spores emitted from a single host and were directed out, up or down; spores were always observed under a coverslip and this may have influenced the orientation of the projections. The range in spore length and arm length appears initially large but these are comparable with other species (range of 50 and 100 μm respectively) (Marquès, 1984; Lom & Dyková, 1992b).

This was the first Triactinomyxon recorded from the marine environment. At least 25 oligochaetes harboured the parasite. Other hosts than *Limnodriloides* cf. *victoriensis* were *Thalassodrilides* sp. (Limnodrilinae) and *Duridrilus* sp. (Phallodrilinae). Infections were difficult to detect without squashing and killing the hosts. Clusters of 3 polar capsules in the intestinal epithelium or a distended intestine are indicative of an infection (Fig. 6B, D). Another 12 oligochaetes had developing Triactinomyxon-like stages in the intestine but no free spores were seen (QM G463607 #203).

Triactinomyxon type 1 nov. (Figs 5, 6)

HOST. Immature limnodriloidine oligochaete.

SITE IN HOST. Posterior gut distended with pansporocysts.

LOCALITY. Boggy Creek, 27°24'S, 153°09'E.

DESCRIPTION. Ovoid spores in pansporocyst become anchor-shaped when exposed to

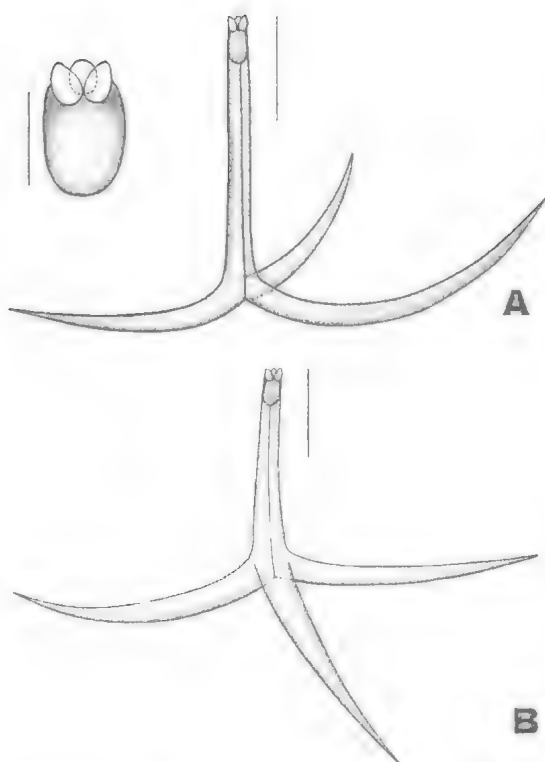


FIG. 5. Drawing of Triactinomyxon types. Side view of spores fully expanded in seawater. A, Triactinomyxon of Roubal et al., 1997. Scale = 50 μ m. [Inset: Spore in intestinal lumen before contact with seawater and valve expansion. Scale = 10 μ m.] B, Triactinomyxon type 1 nov. Scale = 100 μ m.

seawater (Fig. 5B). Polar capsules (8–11 μ m long) remain at anterior end of spore; valve cells form elongated stylus and 3 caudal processes. Spore body (polar capsules plus sporoplasm) 32–44 μ m long (34 μ m, $n=20$) (Fig. 6C) and total spore length 208–268 μ m (236 μ m, $n=20$). Caudal processes, 240–360 μ m long (296 μ m, $n=46$), curve slightly anteriorly, taper to point, α 90°. Suture lines visible, germ cells indiscernible.

REMARKS. Triactinomyxon type 1 closely resembles Triactinomyxon of Roubal et al., 1997, except it is twice the size. When compared to other types (Marquès, 1984 [8 types]; McGeorge et al., 1997 [1 type]; Xiao & Desser, 1998a [6 types]; El-Mansy et al., 1998b, c [9 types]), including those involved in a myxosporean life cycle (El-Matbouli & Hoffmann, 1989, 1993, 1998; Kent et al., 1993; El-Mansy & Molnár, 1997a, b; El-Mansy et al., 1998a; Székely et al., 1999; Eszterbauer et al., 2000), Triactinomyxon

type 1 most closely resembles Triactinomyxon type 4 of El-Mansy et al., 1998c and Triactinomyxon 'E' of Xiao & Desser, 1998a. However, although the length of the processes and polar capsules are similar in type 4 of El-Mansy et al. and our type 1, the average length of the spore body (45 μ m) is greater and the length of the style (149 μ m) less for the former than that of the latter. Similarly, the process length of Triactinomyxon 'E' is within the range of Triactinomyxon type 1, but the polar capsules of the former are smaller (5 μ m) as is the total spore length (spore axis 190–210 μ m).

Triactinomyxon type 2 nov.
(Fig. 7)

HOST. Unidentified tubificid oligochaete.

SITE IN HOST. Not possible to determine if infection is coelomic or intestinal; intestine distended with pansporocyst within its boundary, but the latter may be above rather than within intestine.

TYPE LOCALITY. Boggy Creek, 27°24'S, 153°09'E.

DESCRIPTION. Pansporocyst ~139 μ m across, with 8 subspherical spores (Fig. 7A). Spores fill out into characteristic triactinomyxon anchor-shape after contact with seawater (Fig. 7C). Polar capsules 3, pyriform, ~8 \times 6 μ m, at anterior end of stylus (Fig. 7B). Spore ~346 μ m long, ~38 μ m wide, narrowed anteriorly, posterior end dividing into 3 caudal processes directed posteriorly which taper at ends, ~517 μ m long, α 130°. Sporoplasm within stylus, ~130 μ m long.

REMARKS. The thick stylus and arms are reminiscent of *Siedleckiella* Janiszewska, 1955 but spores of Triactinomyxon type 2 did not appear interconnected either in the pansporocyst or in seawater and arms of *Siedleckiella* are blunt rather than pointed. Triactinomyxon type 2 is larger than any known Triactinomyxon. The arms of *T. magnum* Granata, 1923 are >500 μ m but the stylus is only 25–30 μ m long. The size of the sporoplasm suggests it contains numerous germ cells. Development is asynchronous. Spores were liberated from pansporocysts under pressure. This form was observed on only one occasion and the host worm disintegrated during observation under the cover slip.

Phylum APICOMPLEXA Levine, 1970
Order EUGREGARINORIDA Léger, 1900

Merogony absent; gametogony and sporogony present; typically parasites of annelids and arthropods, but some in other invertebrates.

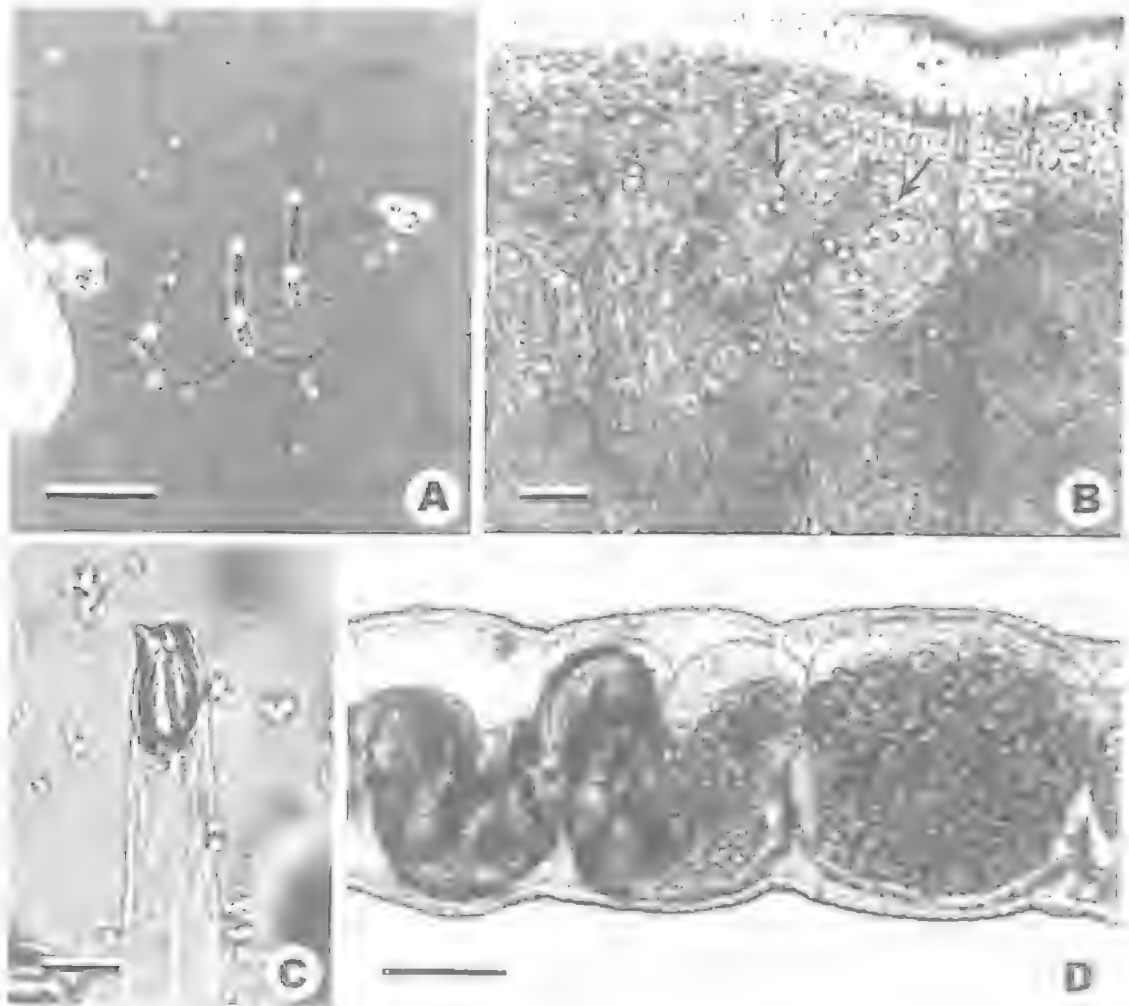


FIG. 6. *Triactinomyxon* spores. Fresh unstained material. A, *Triactinomyxon* of Roubal et al., 1997 spores in seawater. Scale = 125µm. B, prominent polar capsules of *Triactinomyxon* of Roubal et al., 1997 spores within pansporocysts developing in the intestine of an oligochaete. Scale = 20µm. C, anterior end of *Triactinomyxon* type 1 nov. spore in seawater showing polar capsules and sporoplasm. Scale = 20µm. D, intestine of limnodriloidine oligochaete distended with developing stages of *Triactinomyxon* of Roubal et al., 1997. Left side uninfected, right side is filled with pansporoblasts. Scale = 200µm.

Family MONOCYSTIDAE Bütschli, 1882

Gamonts spherical to cylindrical, with anterior end little differentiated if at all; oocysts biconical or navicular; mostly coelomic; the great majority are parasites of oligochaetes.

Genus *Oligochaetocystis* Meier, 1956

Gamonts club-shaped, solitary or in syzygy; syzygy head-to-head [type-species: *O. pachydrili* (Lankester, 1863) Meier, 1956 emend. Levine, 1977].

Oligochaetocystis sp.
(Fig. 8)

HOST. Immature tubificid oligochaete.

SITE IN HOST. All stages coelomic. Several gamonts appeared attached to the oligochaete intestine by their anterior ends. Infection extended from anterior region to middle of oligochaete.

LOCALITY. Boggie Creek, 27°24'S, 153°09'E.

SPECIMEN LODGED. QM G462725 (#147).

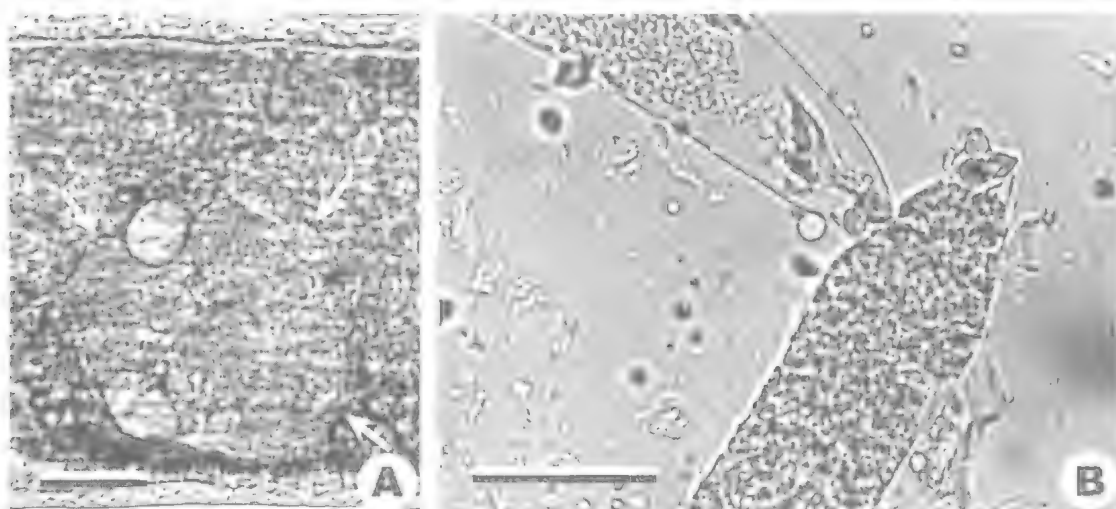
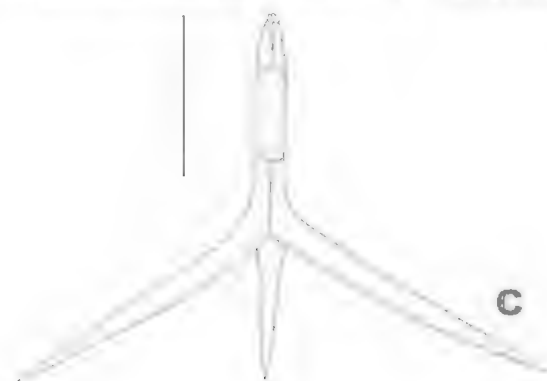


FIG. 7. *Triactinomyxon* type 2 nov. Fresh unstained material. A, Pansporocyst (bound by arrows) in intestine of a limnodriloidine oligochaete. Scale = 50 μ m. B, polar capsules and partial sporoplasm of a spore in seawater. Scale = 40 μ m. C, drawing of side view. Scale = 250 μ m.



DESCRIPTION. Gamonts (trophozoites) club-shaped and aseptate 148-185 (167) \times 31-40 (35) μ m (Table 3). Posterior region paddle-like, narrows into a 'neck' that forms a bulb-like anterior region (Fig. 8A,B). Mucron inconspicuous. Nucleus clear, oval to circular, diameter 6-12 (10) μ m, in mid-posterior region. Gamonts solitary, granular, syzygy not observed. Gametocysts round (diameter 77-96 μ m), containing numerous (100+) gametes (Fig. 8C, D).

REMARKS. This is the only record of *Oligochaetocystis* sp. among the oligochaetes examined. The worm also harboured a coelomic actinosporean, *Sphaeractinomyxon ersei*. *Oligochaetocystis* contains 3 species: *mesenchytraei*, *pachydrili* and *saenuridis* in the coelom of European freshwater oligochaetes; *Mesenchytraeus flavidus*, *Lumbricillus* spp. (Enchytraeidae) and *Tubifex tubifex* (Tubificidae) respectively (Levine, 1977,1988). *O. saenuridis* also occurs in the seminal vesicles.

Phylum CILIOPHORA Doflein, 1901

Internal ciliates were most prevalent in worms from Heron Is.; infected worms were rare in Moreton Bay and were represented usually by a single ciliate. In contrast, ectocommensal ciliates, represented by *Scyphidia* sp., were found only on Moreton Bay oligochaetes.

Class OLIGOHYMENOPHORA de Puytorac et al., 1974

Order ASTOMATIDA Schewiakoff, 1896

Large body; uniformly ciliated; mouthless; endosymbiotic in oligochaetes, polychaetes, leeches, free-living flatworms and molluscs.

Family RADIOPHRYIDAE de Puytorac, 1972

Body flattened; V-shaped apical cytoskeletal organelle; dense somatic ciliation.

Radiophrya sp. (Fig. 9A-C)

HOST. Tubificid oligochaetes.

SITE IN HOST. Intestinal lumen, near clitellar region (Fig. 9A).

SPECIMENS LODGED. QM G463608 (H116), G463609 (H133).

LOCALITY. Heron Is., 23°27'S, 151°55'E.

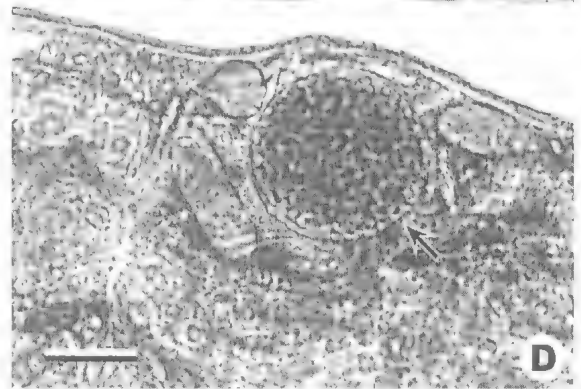
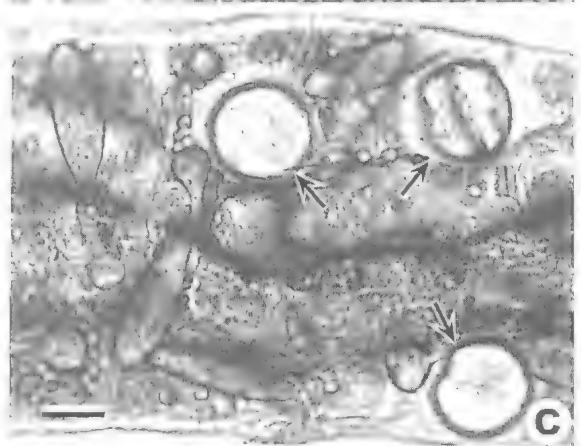
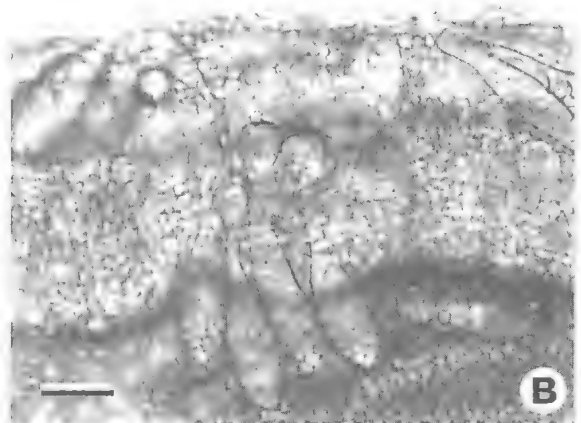
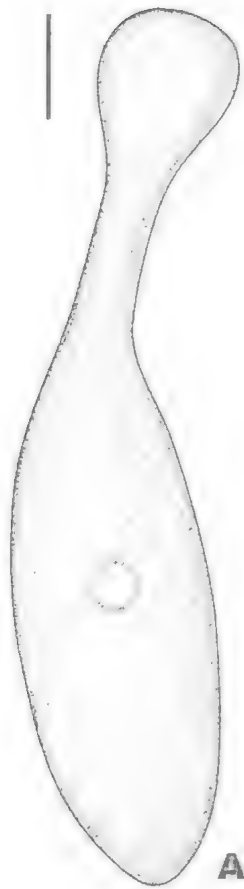


FIG. 8. *Oligochaetocystis* sp. in the coelom of an immature tubificid oligochaete. Fresh unstained material. A, drawing of a gamont. Scale = 20 μ m. B, Gamonts. Scale = 50 μ m. C, early gametocysts (arrows). Scale = 50 μ m. D, Gametocyst (arrow) containing numerous gametes. Scale = 50 μ m.

DESCRIPTION. Body elongate, straight to curved, 140-180 μ m long, tapering posteriorly and anteriorly, V-shaped attachment structure anteriorly, arms of V of about equal length, longitudinal kineties converge at each end; macronucleus large; much of one surface reinforced by cortical fibres extending almost whole length of body (Fig. 9B, C).

REMARKS. Endocommensal, up to 30 per host. Cilia beating.

Unidentified astomate ciliates
(Fig. 9D-F)

HOST. *Grania* sp. (Enchytraeidae)

LOCALITY. Heron Is., 23°27'S, 151°55'E.

SITE IN HOST. Intestinal lumen (Fig. 9D).

SPECIMEN LODGED. QMG463610 (H153).

DESCRIPTION. Ciliates elongate, 177–257 μm long, 65 μm wide, posteriorly tapered, anteriorly blunt, oral structures (vestibulum, cytostome, trichites) absent, no prominent anterior attachment region or structures such as suckers, hooks or spines; macronucleus elongate ribbon-like; kineties longitudinal, ~10 rows (Fig. 9E, F). Budding not observed.

REMARKS. All characters conform to those of the Astomatida but none conforms exactly to any of the 8 families of astomate ciliates known from aquatic and terrestrial annelids. Apparent lack of an anterior attachment structure is consistent with the Anoplophryidae but most species in this family are large (>300 μm) and have about 40–100 kineties, whereas the present ciliates are up to 260 μm long and have only 10 longitudinal kineties. Species belonging to all other families have distinctive attachment organelles. At least 6 ciliates inhabited the worm with only 1 per segment.

Order PERITRICHIDA Stein, 1859

Body goblet-shaped; conspicuous oral ciliature winding counter-clockwise to cytostome; scopula antapical; widespread throughout aquatic habitats; many free-living or symphorionts on diverse hosts; some commensals or parasites.

Family SCYPHIDIIDAE Kahl, 1933

Solitary zooids; stalkless; disc-like scopula; generally found as epibionts mainly on invertebrates.

Scyphidia sp. (Fig. 10)

HOST. Limnodriloidine oligochaetes.

SITE IN HOST. Attached to posterior integument (Fig. 10A).

LOCALITY. Boggy Creek, Moreton Bay, 27°24'S, 153°09'E.

DESCRIPTION. Zooid bell-shaped, ~40–50 μm long, aloricate, stalk absent; scopula sessile, solitary (but can occur in close proximity to each other), macronucleus U-shaped (Fig. 10A).

REMARKS. This ectocommensal ciliate was found attached to the posterior region of

TABLE 3. Morphometric characters of the gregarine *Oligochaetocystis* sp.

	Mean (μm)	Minimum (μm)	Maximum (μm)	No. observations
GAMONT				
Length	166.9	148.3	185.4	8
Width	34.8	30.9	40.2	8
Neck width	10.3	7.7	13.9	8
Bulb width	24.7	24.7	24.7	3
Bulb length	25.7	21.6	27.8	3
Nucleus diameter	10.3	6.2	12.4	3
GAMETOCYST				
Larva	81.4	77.3	86.5	3
Late	95.8	-	-	1

oligochaetes from muddy habitats but was never associated with oligochaetes from the coral reef. About 10 ciliates were present simultaneously on a worm either singly or in small groups of 2–5 zooids. *Scyphidia* spp. attach to both vertebrates and invertebrates as well as to submerged objects; about 19 species have been recorded.

Phylum HAPLOSPORIDIA Caullery & Mesnil, 1889

Histozoic, coelozoic unicellular parasites which form unicellular, typically uninucleated distinctive propagules, 'spores' without polar capsules or polar filaments (Perkins, 1990).

Haplosporidium sp. (Fig. 10)

HOST. Tubificid oligochaetes (including *Heterodrilus* sp.).

SITE IN HOST. Intestinal epithelium, free spores in intestinal lumen.

LOCALITY. Heron Is., 23° 27'S, 151° 55'E.

SPECIMENS LODGED. QM G463611 (H97), QM G463612 (H147).

DESCRIPTION. Unicellular spore without polar capsule or polar filament. Spores irregularly shaped, round to oval, 8–10 \times 13–15 μm , groups of about eight enclosed by membrane (pansporoblast ~23 μm) (Fig. 10B). Spores possess characteristic operculum-like caps.

REMARKS. Haplosporidia were first believed to be actinosporeans because of the arrangement of the spores in groups of eight in the intestine; however, they do not contain polar capsules. Sixteen of the 2,000 oligochaetes examined from Heron Is. harboured *Haplosporidium* sp.

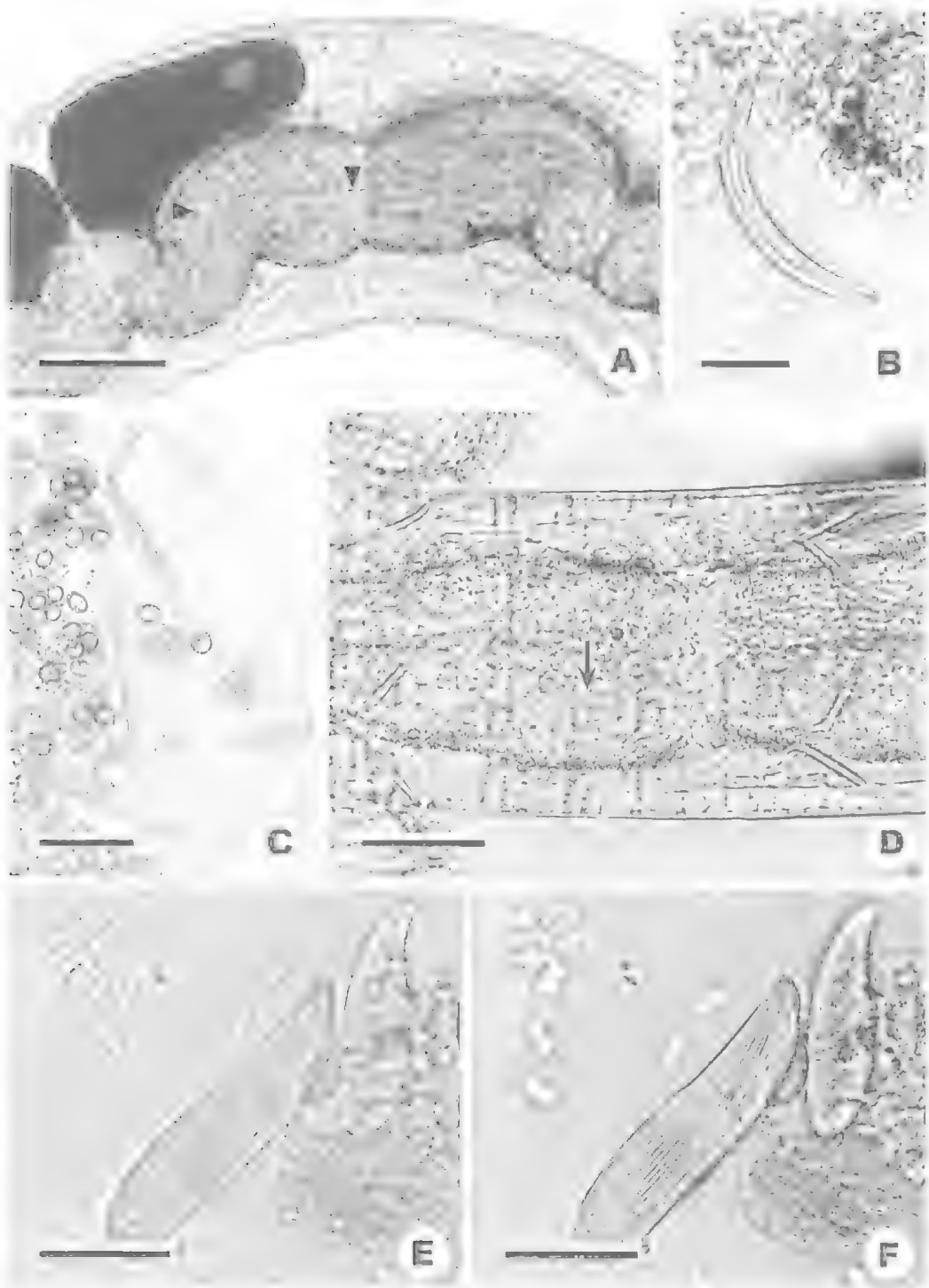


FIG. 9. Astomate ciliates. A-C, *Radiophyra* sp. D-F, unidentified, from the intestinal lumen of oligochaetes at Heron Island. Fresh unstained material. A, ciliates in intestinal lumen of a tubificid oligochaete (arrowheads). Scale = 150µm; B, curved ciliate in seawater. Scale = 50µm; C, elongate ciliates in sea water. Scale = 100µm; D, ciliate (arrow) in the intestinal lumen of an enchytraeid oligochaete. Scale = 100µm; E, ciliate in seawater with macronuclei in focus. Scale = 100µm; F, same ciliates with somatic kinetics in focus. Scale = 100µm.

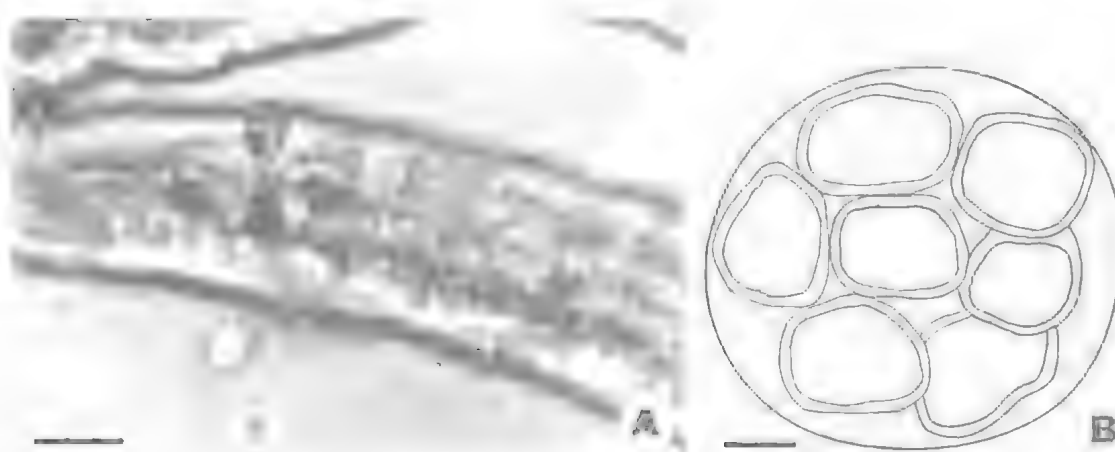


FIG. 10. Protozoans from marine oligochaetes. A, *Scyphidia* sp. contracted zooids attached to posterior region of limnodriloidine oligochaete. Fresh unstained material. Scale = 50µm; B, *Haplosporidium* sp. pansporoblast containing eight spores. Scale = 5µm.

Phylum APICOMPLEXA Levine, 1970
Class COCCIDEA Leuckart, 1879

Life cycle with merogony, gamogony and sporogony; producing small intracellular gamonts, single macrogamete; monoxenous or heteroxenous parasites in vertebrates and invertebrates.

Unidentified coccidian (Fig. 11)

HOST. Tubificid oligochaetes including Limnodriloidinae sp.

SITE IN HOST. Primarily coelomic but the parasites appear to 'bud off' from intestine (Fig. 11A).

LOCALITY. Moreton Bay, 27°15'-25'S

DESCRIPTION. Oocysts not seen or not present, sporocysts spherical, 12-16µm (14µm, n=8) in diameter; contain ~16 sporozoites, roughly spherical, ~3µm across (Fig. 11A-C). Meronts and gamonts not observed.

REMARKS. An accurate record of prevalence was not maintained. Parasites were recorded also from the posterior part of the gut. Some sporocysts were observed to 'excyst' in seawater (Fig. 11D). The cysts resemble those of the protococcidian *Grellia* Levine, 1973 which has ellipsoidal sporocysts 12-14µm long, contain 5-14 sporozoites and which inhabits the coelom of archiannelids and polychaetes. The specimens we found had neither ellipsoidal oocysts nor large gamonts. The sporocysts may represent a hitherto unidentified eucoccidian genus.

Phylum NEMATODA
Class ENOPLEA
Order MERMITHIDA
Family MERMITHIDAE

Adult worms free-living; juveniles parasitic in body cavity of various invertebrates, primarily insects; no functional gut at any stage.

Unidentified mermithid nematodes (Fig. 12)

HOST. *Heterodrilus* cf. *keenani* and possibly other tubificid taxa.

SITE IN HOST. Coelom, in posterior part of host.

LOCALITY. Heron Is., 23° 27'S, 151° 55'E.

SPECIMEN LODGED. QM G218270 (H145).

DESCRIPTION. Two types of mermithid nematodes were observed; both juvenile (no gonads) and coiled in the host (Fig. 12). Width uniform along length. Anterior end blunt, posterior end tapered to a point. Buccal cavity, short, narrow, anterior end rounded, reminiscent of ascarophid nematodes. Pharynx, not well defined; lips absent. One nematode type long with green intestine, four specimens, length 1,400-2,064µm, width 30-41µm (Fig. 12A). Second type short, without pigmentation, two specimens, length 244-1,080µm, width 10-35µm (Fig. 12B).

REMARKS. Four oligochaetes each harboured 1 nematode and a fifth oligochaete held 2 nematodes, one of each type. The nematodes were fixed inside the oligochaete host. Some

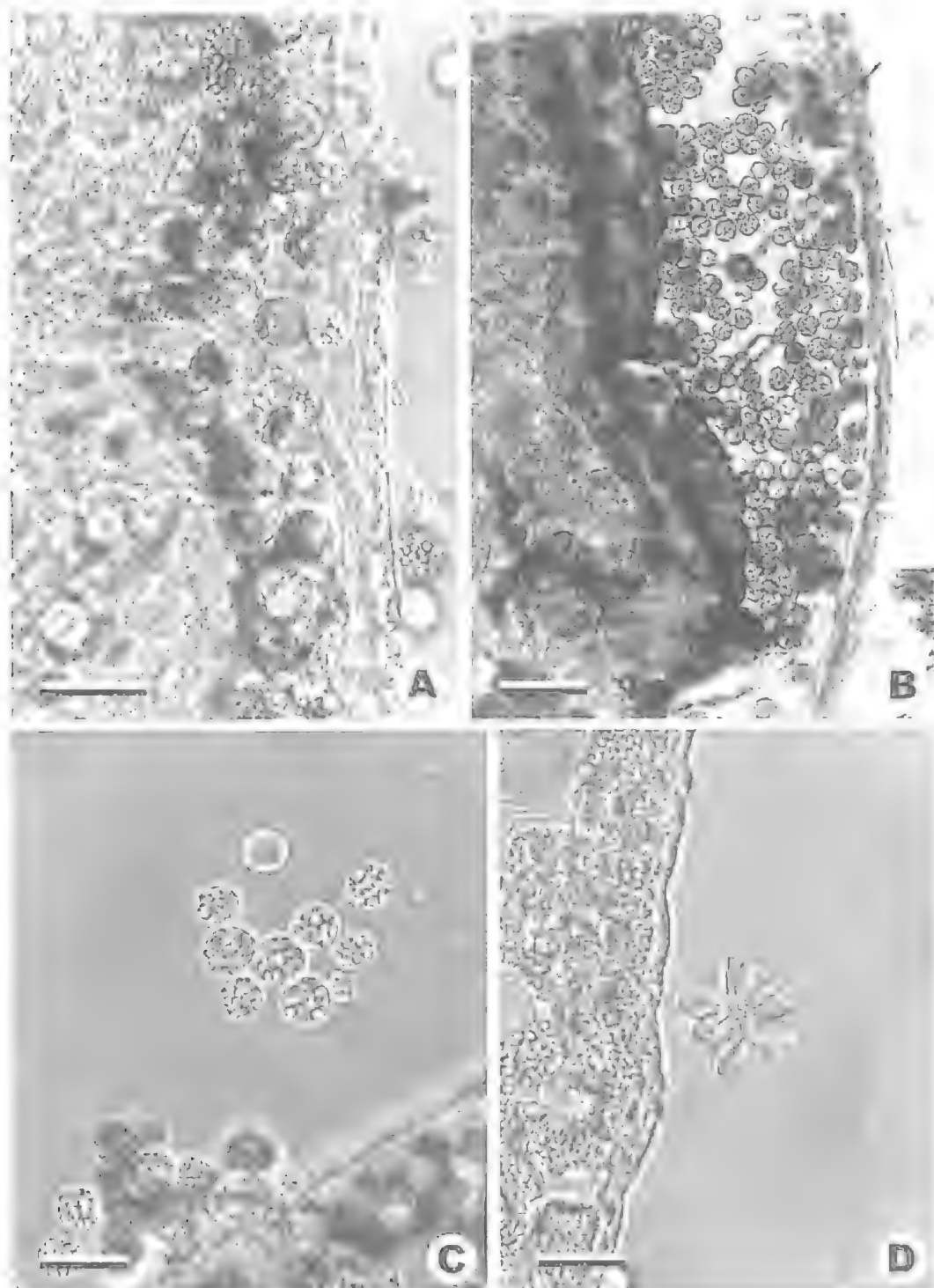


FIG. 11. Unidentified coccidian from limnodriloidine oligochaete. Fresh unstained material. A, coccidian sporoblasts 'budding-off' intestinal epithelium into coelom. Scale = $30\mu\text{m}$; B, numerous sporocysts in coelom. Scale = $50\mu\text{m}$; C, sporocysts in seawater. Scale = $25\mu\text{m}$; D, excysted sporocyst with sporozoites netted in seawater. Scale = $25\mu\text{m}$.

were then cleared and stained with chlorolactophenol and Mayer's haemotoxylin but this did not facilitate identification of them.

DISCUSSION

Australian marine oligochaetes were found to be infected with a range of metazoan and protozoan parasites/commensals (Tables 1, 2). Tubificids dominated the oligochaete samples and although enchytraeids comprised at least 11% of the Heron Is. collections, only one worm was infected (*Grania* sp. with an astomate ciliate). Members of the tubificid *Limnodriloidinae*, *Phallodrilinae* and *Rhyacodrilinae* were infected with actinosporeans, ciliates, haplosporidians, coccidians, nematodes and gregarines. While double infections with species from the same parasite group were rare, infections by two parasites belonging to different groups were not uncommon; e.g. actinosporeans and ciliates or actinosporeans and gregarines.

MYXOZOA. The actinosporeans we described (except possibly *Triactinomyxon* of Roubal et al., 1997) have been found only in Australia. Marine actinosporeans do not exhibit the same degree of host specificity as do freshwater actinosporeans and most (>60%) infect 2 or more marine oligochaetes e.g. *Sphaeractinomyxon ersei* was recorded from *Doliodrilus*, *Limnodriloides*, *Thalassodrilides* and *Bathydrilus*. Conversely, a species of marine oligochaete may be host to several actinosporean types. e.g. *Thalassodrilides* is infected by both *S. ersei* and *Endocapsa rosulata* but, as far as we have observed, not simultaneously. In contrast, 90% of freshwater actinosporeans occur in only one oligochaete species (cf. Marquès, 1984; Xiao & Desser, 1998c). One oligochaete species, however, may be host to several actinosporeans e.g. *Tubifex tubifex* is host to at least 12 types represented by 7 collective groups: *Neoactinomyxon*, *Guyenotia*, *Echinactinomyxon*, *Raabeia*, *Triactinomyxon*, *Hexactinomyxon* and *Synactinomyxon*.

The role of actinosporeans in marine oligochaetes is not yet fully understood but both are implicated in the life cycle of marine myxosporeans. Of particular importance are members of the myxosporean genus *Kudoa* that dwell in the skeletal muscles of marine fish and cause economic losses in mariculture around the world (Ireland, USA, Canada and Australia) (see Kent et al., 1994b; Palmer, 1995; Hallett et al., 1997b). Knowledge of the biology of the

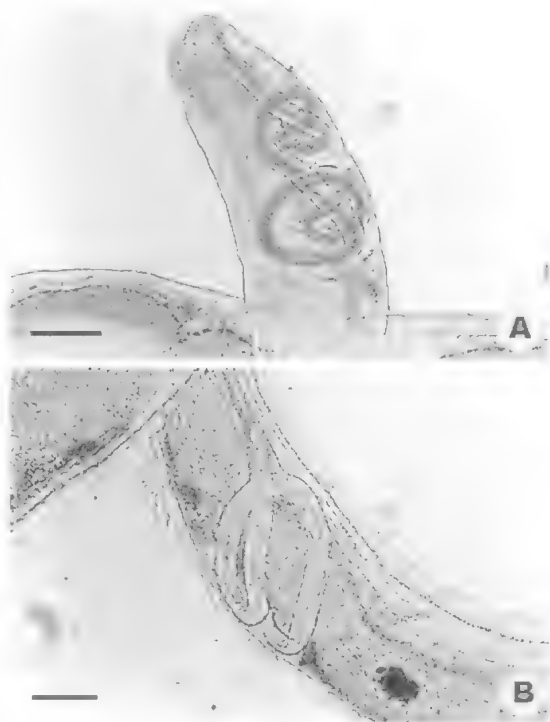


FIG. 12. Mermithid nematodes in posterior coelom of oligochaetes from Heron Island. Fresh unstained material. A, green mermithid nematode. Scale = 100µm. B, clear mermithid nematode. Scale = 100µm.

parasite, including its life cycle, is required to control and alleviate these problems. Despite evidence that at least 24 freshwater myxosporeans alternate with an actinosporean stage in an oligochaete, similar connections (or any others) have not been established for any marine myxosporeans or actinosporeans. Indeed, Diamant (1997) provides experimental evidence for direct fish-to-fish transmission of at least 1 species, *Myxidium leei*, which would theoretically eliminate the need for an alternate invertebrate host (Diamant, 1997); though this direct transmission may alternate with transmission via actinospores (Lom & Dyková, 1995).

Significant changes were proposed for the taxonomic treatment of actinosporeans during the course of our studies. The result of conclusions made by Kent et al. (1994a) that alternate myxosporean development probably occurs in all actinosporean families and genera, was the proposal that nominal actinosporean generic names should not be distinguished from

myxosporean genera and, consequently, all actinosporean genera and species be declared invalid (except *Tetractinomyxon*) thereby treating their nominal generic names as collective group names. The majority of actinosporean descriptions postdating these proposals adopt them without comment (McGeorge et al., 1997; Xiao & Desser, 1998; El-Mansy et al., 1998b,c). Various researchers over the past two decades have proposed the redundancy, either partly or fully, of every taxonomic level within the Myxozoa, notwithstanding the phylum itself (Kent et al., 1994a; Siddall et al., 1996). The Myxozoa are now recognised generally as being Metazoa, although their exact placement within this group is still unclear. Because the position of most actinosporeans within the phylum is currently uncertain, and for the sake of consistency, we employ the identification system recommended by Kent et al. (1994a) and Lom et al. (1997), although we would prefer to ascribe a binomial identity to actinosporean forms that do not have clear links to myxosporean genera. We have added 'nov.' at the start of descriptions of previously undescribed forms to avoid confusion between new forms and those already described (cf. El-Mansy et al., 1998c).

Prior to this study, marine actinosporeans had been described from France (*S. stolci* from the oligochaete *Clitellio arenarius* and *Hemitubifex benedini* (= *Tubificoides benedii*) (Caullery & Mesnil, 1904; Marquès, 1984)), Romania (*S. stolci* from *Tubifex* sp. (Radulescu & Motilicia, 1957)), England (*Tetractinomyxon intermedium* and *T. irregulare* from the sipunculid worm *Petalostoma minutum* (Ikeda, 1912)) and Hong Kong (*Aurantiactinomyxon* type 1 & 2 from *Pacifidrilus vanus*, *Aurantiactinomyxon* type 2 from *P. darvelli* and *Limnodriloides toloensis*, *Sphaeractinomyxon* type 1 from *Aktedrilus mortoni* and *Sphaeractinomyxon* type 2 from *Aimodrilus geminus* (Hallett et al., 1997a)). We have now observed marine actinosporeans not only in Australian tubificid oligochaetes but also marine oligochaetes from: near Honiara, Solomon Islands (Tubificidae sp. (unidentified), Limnodriloidinae sp. and *Heterodrilus* sp.); Jiaozhou Bay, near Qingdao, China (*Doliodrilus tener*); Florida, USA (*Tectidrilus squalidus*); and Ascension Island, South Atlantic (*Thalassodriloides gurwitschi*) (all material retrieved from second author's collection; unpubl. data).

This study demonstrates that actinosporeans occur in marine oligochaetes, and these findings

will facilitate experimental and molecular studies into the life cycle and systematics of this group.

Infections in oligochaetes could not be detected on the basis of differences in worm motility, colour, size or shape. Instead, coelomic infections were readily discerned by the presence of iridescent spheres in the coelom when examined using incident light under a dissection microscope (the refractile bodies representing pansporocystic stages of the actinosporeans). The sporogonic stages varied considerably in size and internal composition and were more difficult to recognise, but the presence of numerous mature spores, monomorphic in appearance, was indicative of infection. Light microscopy generally revealed the coelom to be packed with pansporocysts in coelomic infections or the intestine to be distended with pansporocysts in gut infections. Similar distension has been reported also by Janiszewska (1955). Wolf et al. (1986), however, found the intestinal (freshwater) actinosporean *Triactinomyxon gyrosalmo* to be abundant in worms that were pale, had generalised anterior swellings and displayed an opaque outer layer. Similarly, Molnár et al. (1999a) could distinguish tubificids heavily infected with raabeia to be pale in colour and move sluggishly, El-Matbouli & Hoffmann (1993) recognised triactinomyxon infected tubificids by their whitish discolouration and Molnár et al. (1999b) noted that intestinal segments infected with neoactinospores appeared darker in colour and had thickened walls compared to uninfected areas. In contrast, Yokoyama et al. (1991) found that *Raabeia* sp. infections, apparently in the body cavity of the freshwater tubificid *Branchiura sowerbyi*, were not visible externally. We found coelomic infections to develop anteriorly in an oligochaete with more advanced stages located more posteriorly as the infection developed. El-Mansy et al. (1998a) observed triactinospores in the centrally located intestinal segments in moderate infections but in most segments when severe.

The findings presented in this review support the literature that natural actinosporean infections have a low prevalence in oligochaetes being 0.1–9.5% (Mackinnon & Adam, 1924; Hamilton & Canning, 1987; Yokoyama et al., 1991, 1993a, 1993b; McGeorge et al., 1997; Hallett et al., 1998; Xiao & Desser, 1998c; Özer & Wootten, 2000). An exception is the findings of El-Mansy et al. (1998c) who recorded a significantly higher prevalence of up to 43% which they attributed to their examination

technique. Mixed infections are reported to be rare (Yokoyama et al., 1991; Xiao & Dessler, 1998c) and indeed, only one of the 222 infected worms of the present study harboured two actinosporean species. In experimental infections, prevalences of 3 to almost 100 percent have been observed (Wolf et al., 1986; Kent et al., 1993; Yokoyama et al., 1993a; Uspenskaya, 1995; El-Mansy et al., 1997b; El-Mansy et al., 1998a; Molnár et al. 1999a,b; Özer & Wootten, 2000). Coelomic actinosporeans accounted for most infections (>80%) and *Sphaeractinomyxon ersei* represented 23.9% of all infected worms from Moreton Bay. In contrast, all 25 actinosporeans recorded by Xiao & Dessler (1998c) parasitised the intestinal epithelium. Gut-inhabiting actinosporeans like *Neoactinomyxum*, *Guyenotia* and *Hexactinomyxon* spp., are common in freshwater oligochaetes, however the only gut-inhabiting actinosporeans we identified were forms of *Triactinomyxon*. There was no obvious seasonal influence on infections; the highest prevalence (12.1%) was recorded in June at Boggy Creek and the lowest (0.47%) in May at Scott Point. A number of other studies, however, have reported temporal patterns (see Yokoyama et al., 1993; Xiao & Dessler, 1998c; El-Mansy et al., 1998c; Özer & Wootten, 2000).

Most infected oligochaetes were sexually immature, which hindered identification of the host. It is not known whether the presence of actinosporeans and other parasites may adversely affect the maturation of oligochaetes. Sexually mature worms, however, constitute only a small part of populations of marine oligochaetes at most times (Erséus, 1994).

Different fixatives (including ethylalcohol, Bouin's, Trump's, glutaraldehyde and Karnovsky's) were used to preserve infected worms, depending upon their intended use. These chemicals had varying effects on actinosporean spores when combined with the stain paracarmine and the mounting process which were necessary to identify the host worms. Karnovsky's fixative preserved spores best even though they had 'shrunk' by 1–2 µm (3.5%); all other fixatives resulted in greater shrinkage of the spores. *Endocapsa* specimens were affected to a greater extent than *Sphaeractinomyxon* or *Tetraspora* types, related perhaps to the valve cell properties of these groups; *Endocapsa* species have valve cells that swell whereas those of *Sphaeractinomyxon* and *Tetraspora* types do not (see Hallett et al., 1998; Hallett et al., 1999; Hallett & Lester, 1999). Detailed drawings

accompanied with a range of micrographs are therefore recommended (see also Lom et al., 1997). Material fixed in Bouin's or Trump's fixative, but not processed further, appear to be representative but spores become deformed and distorted when stained and mounted. A complete taxonomic description requires information about: mature spores observed both in the host and free in seawater (or freshwater) to monitor changes in size and shape; the host stained in alcoholic paracarmine and mounted whole in Canada Balsam preferably after fixation in Bouin's solution; and developing stages and where they are located in the host and their appearance. The anterior part of the oligochaete fixed separately in Bouin's solution is needed to check host identity regardless of the intended use of the infected worm for either histology, TEM or DNA studies.

APICOMPLEXA. Gregarines are widespread, common parasites of invertebrates, particularly arthropods. New hosts ingest gametocysts and the oocysts they contain, to become infected. The low prevalence of gregarines in marine oligochaetes suggests they may be an atypical host group; nevertheless gregarines formed gametocysts and developed. Apparently, oocysts were ingested and sporozoites migrated across the gut epithelium into the body cavity of the host worm where they underwent gamogony, but neither oocysts containing sporozoites nor syzygy were observed. We believe this to be the first record of a marine tubificid oligochaete infected with a gregarine, but enchytraeids infected by monocystid gregarines dominate the records (Giere & Pfannkuche, 1982).

CILIOPHORA. In this study, most ciliates were fixed *in situ* within worms so that the hosts could be identified. Subsequent dissections of infected worms yielded few intact ciliates and silver impregnation studies were uninformative. None of the ciliates were therefore identified to species level. Nonetheless, the ciliates were clearly astomate and peritrichous species as determined by their morphological characters. Similar groups occur as endo- or ecto- commensals in oligochaetes (Giere & Pfannkuche, 1982). Ciliates should be carefully extracted from host tissues and observed live to note colour, rigidity, motility, contractile vacuole, location, etc. Ciliates should then be fixed in Bouin's, Stieve's or Dafano's fluid prior to silver impregnation to reveal patterns of ciliation, attachment structures, nuclear arrangement, etc. Regrettably, the best

silver stain to use for any particular ciliate group can vary considerably so it is advisable to use multiple stains including silver nitrate, silver carbonate and silver proteinate. The prevalences and intensities of infection by internal ciliates were lower in Moreton Bay than at Heron Island. External ciliates, however, were observed only on worms from Moreton Bay, particularly those collected at Boggy Creek with substantial silt loads compared to the pristine coral cay of Heron Island; the parasite fauna reflects this difference. Similar external ciliates (order Sessilida) were reported from *Limnodriloides biforis* Erséus, 1990 in muddy sediments associated with estuarine habitats in Hong Kong (Erséus, 1990). *Grania* spp. (Enchytraeidae) for some reason seem untouched by the parasites which were relatively prevalent in marine tubificids.

NEMATODA. Oligochaetes are phoretic, paratenic, intermediate and definitive hosts for nematodes (Poinar, 1978; Smith, 1985). Juvenile mermithid nematodes primarily infect insects but also molluscs, crustaceans, arachnids and other invertebrates; mermithid adults are free-living (Poinar, 1976). The juvenile emerges from the egg, penetrates into the body cavity of an invertebrate host, develops for a period to emerge finally into the environment where it moults to the adult stage. Mermithids almost always kill their host (Poinar, 1976); the large size of the nematodes relative to their oligochaete host observed in the current study imply a similar life cycle for the mermithids we found.

The majority of associations of nematodes and oligochaetes are with earthworms (Poinar, 1978). Only 1 of the 83 species cited in Poinar (1978) was a tubificid (freshwater) oligochaete and its nematode was listed as unidentified. Smith (1985) subsequently documented at least 3 microdrile families as hosts to this group; these were Lumbriculidae, Naididae and Tubificidae to members of Diotrophmatidae, Rhabditidae, Anisakidae and Mermithidae. Smith (1985) found Mermithidae usually in the anterior half of the naidid oligochaetes examined. All six nematodes we found were located posteriorly in the tubificid oligochaetes. Smith (1985) considered migration to be unlikely but rather assumed that the larvae hatched quickly from ingested eggs, penetrated the gut and then resided in the anterior portion of the worm. No more than two nematodes were observed per worm in either study and Smith (1985) recorded that the total

prevalence of infection was low and concluded that naidid infections were probably incidental.

Parasitology of marine oligochaetes is fertile ground for studies and we made many new records of infection. The diverse range of organisms detected in oligochaetes indicate that worms are susceptible to external, intestinal and coelomic infections by both commensal and parasitic species. The host range, geographic distribution, habitat requirements and specificity of infection for parasites of marine oligochaetes remain to be determined.

ACKNOWLEDGEMENTS

We thank Ms Kylie Jennings and Mr Stephen Atkinson for collecting assistance in Moreton Bay and Heron Island and Dr Rob Adlard for providing the NSW sample; and Ms Barbro Löfnertz and Mrs Anna Hedström for staining and mounting oligochaete specimens. Assistance with digital imaging from Mr Atkinson is appreciated also. Financial support came from a University of Queensland Postgraduate Research Scholarship to SLH, an Australian Research Council grant (# A195065) to RJGL and Swedish Natural Science Research Council to CE.

LITERATURE CITED

- CAULLERY, M. & MESNIL, F. 1904. Sur un type nouveau (*Sphaeractinomyxon stolci* n.g. n.sp.) d'Actinomyxidies, et son développement. Comptes rendus des séances de la Société de biologie Paris 56: 408-410.
- DIAMANT, A. 1997. Fish-to-fish transmission of a marine myxosporean. Diseases of Aquatic Organisms 30: 99-105.
- EL-MANSY, A. & MOLNÁR, K. 1997a. Extrapiscine development of *Myxobolus drjagini* Akhmerov, 1954 (Myxosporae: Myxobolidae) in oligochaete alternative hosts. Acta Veterinaria Hungarica 45: 427-438.
- 1997b. Development of *Myxobolus hungaricus* (Myxosporae: Myxobolidae) in oligochaete alternate hosts. Diseases of Aquatic Organisms 31: 227-232.
- EL-MANSY, A., MOLNÁR, K. & SZÉKELY, C.S. 1998a. Development of *Myxobolus portucalensis* Saraiva & Molnár, 1990 (Myxosporae: Myxobolidae) in the oligochaete *Tubifex tubifex* (Müller). Systematic Parasitology 41: 95-103.
- EL-MANSY, A., SZÉKELY, C.S., MOLNÁR, K. 1998b. Studies on the occurrence of actinosporean stages of fish myxosporeans in a fish farm of Hungary, with the description of triactinomyxon, raabeia, aurantiactinomyxon and neoactinomyxon types. Acta Vet Hungarica 46:259-284.

- 1998c. Studies on the occurrence of actinosporean stages of myxosporeans in Lake Balaton, Hungary, with the description of triactinomyxon, raabeia, and aurantiactinomyxon types. *Acta Vet Hungarica* 46: 437-450.
- EL-MATBOULI, M. & HOFFMANN, R.W. 1989. Experimental transmission of two *Myxobolus* spp. developing bisporogeny via tubificid worms. *Parasitology Research* 75: 461-464.
1993. *Myxobolus carassii* Klokaceva, 1914 also requires an aquatic oligochaete, *Tubifex tubifex* as an intermediate host in its life cycle. *Bulletin of the European Association of Fish Pathologists* 13: 189-192.
1998. Light and electron microscopic studies on the chronological development of *Myxobolus cerebralis* to the actinosporean stage in *Tubifex tubifex*. *International Journal for Parasitology* 28: 195-217.
- ERSEÜS, C. 1976. Littoral Oligochaeta (Annelida) from Eyjaförður, north coast of Iceland. *Zoologica Scripta* 5: 5-11.
1990. Marine Oligochaeta of Hong Kong. Pp. 259-335. In Morton, B. (ed.) *Proceedings of the Second International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong and Southern China*, Hong Kong, 1986. (Hong Kong University Press: Hong Kong).
1994. The Oligochaeta. Pp. 5-38. In Blake, J.A. & Hilbig, B. (eds) *Taxonomic atlas of the Santa Maria Basin and western Santa Barbara Channel*. Vol. 4 - The Annelida Part 1. Oligochaeta and Polychaeta: Phyllodocida (Phyllodocidae to Paralacydoniidae). (Santa Barbara Museum of Natural History: Santa Barbara, California).
- ESZTERBAUER, E., SZÉKELY, C.S., MOLNÁR, K. & BASKA, F. 2000. Development of *Myxobolus bramaie* (Myxosporea: Myxobolidae) in an oligochaete alternate host, *Tubifex tubifex*. *Journal of Fish Diseases* 23: 19-25.
- GIERE, O. & PFANNKUCHE, O. 1982. Biology and ecology of marine Oligochaeta, a review. *Oceanography and Marine Biology, an Annual Revue* 20: 173-308.
- HALLETT, S.L., ERSEÜS, C. & LESTER, R.J.G. 1995. An actinosporean from an Australian marine oligochaete. *Bulletin of the European Association of Fish Pathologists* 15: 168-171.
- 1997a. Actinosporea from Hong Kong marine Oligochaeta. Pp. 1-7. In Morton, B. (ed.) *Proceedings of the Eighth International Marine Biological Workshop: the Marine Flora and Fauna of Hong Kong and Southern China*, Hong Kong, 2-20 April, 1995. (Hong Kong University Press: Hong Kong).
1999. Actinosporeans (Myxozoa) from marine oligochaetes of the Great Barrier Reef. *Systematic Parasitology* 44: 49-57.
- HALLETT, S.L. & LESTER, R.J.G. 1999. Actinosporeans (Myxozoa) with four developing spores within a pansporocyst: *Tetraspora discoidea* n. g. n. sp. and *Tetraspora rotundum* n. sp. *International Journal for Parasitology* 29: 419-427.
- HALLETT, S.L., O'DONOGHUE, P.J. & LESTER, R.J.G. 1997b. Infections by *Kudoa ciliatae* (Myxozoa: Myxosporea) in Indo-Pacific whiting *Sillago* spp. *Diseases of Aquatic Organisms* 30: 11-16.
1998. Structure and development of a marine actinosporean, *Sphaeractinomyxon ersei* n. sp. (Myxozoa). *Journal of Eukaryotic Microbiology* 45: 142-150.
- HAMILTON, A.J. & CANNING, E.U. 1987. Studies on the proposed role of *Tubifex tubifex* (Müller) as an intermediate host in the life cycle of *Myxosoma cerebralis* (Hofer, 1903). *Journal of Fish Diseases* 10: 145-151.
- IKEDA, I. 1912. Studies on some Sporozoan parasites of Sipunculoids. *Archiv für Protistenkunde* 25: 240-272.
- JANISZEWSKA, J. 1955. Actinomyxidial. Morphology, ecology, history of investigations, systematics, development. *Acta Parasitologica Polonica* 2: 405-437.
1957. Actinomyxidial II. New systematics, sexual cycle, description of new genera and species. *Zoologica Polonica* 8: 3-34.
- KENT, M.L., MARGOLIS, L. & CORLISS, J.O. 1994a. The demise of a class of protists: taxonomic and nomenclatural revisions proposed for the protist phylum Myxozoa Grassé, 1970. *Canadian Journal of Zoology* 72: 932-937.
- KENT, M.L., MARGOLIS, L., WHITAKER, D.J., HOSKINS, G.E. & MCDONALD, T.E. 1994b. Review of Myxosporea of importance in salmonid fisheries and aquaculture in British Columbia. *Folia Parasitologica* 41: 27-37.
- KENT, M.L., WHITAKER, D.J. & MARGOLIS, L. 1993. Transmission of *Myxobolus arcticus* Pugachev & Khokhlov, 1979, a myxosporean parasite of Pacific salmon, via a triactinomyxon from the aquatic oligochaete *Stylodrilus heringianus* (Lumbricidae). *Canadian Journal of Zoology* 71: 1207-1211.
- KOSTE, W. 1970. Über eine parasitische Rotatorienart *Albertia reichelti* nov. spec. *Zoologischer Anzeiger* 184: 428-434.
- LEVINE, N.D. 1977. Revision and checklist of the species of the aseptate gregarine family Monocystidae. *Folia Parasitologica (Praque)* 24 (1).
1988. The protozoan phylum Apicomplexa, 1. (CRC Press Inc.: Florida).
- LOM, J. 1990. Phylum Myxozoa. Pp. 36-52. In Margolis, L., Corliss, J.O., Melkonian, M. & Chapman, D.J. (eds) *Handbook of protozoists*. (Jones & Bartlett: Boston).
- LOM, J. & DYKOVÁ, I. 1995. Myxosporea (Phylum Myxozoa). Pp. 97-148. In Woo, P.T.K. (ed.) *Fish diseases and disorders Volume 1: Protozoan and Metazoan infections*. (CAB International: United Kingdom).

- LOM, J., McGEORGE, J., FEIST, S.W., MORRIS, D. & ADAMS, A. 1997. Guidelines for the uniform characterisation of the actinosporean stages of parasites of the phylum Myxozoa. *Diseases of Aquatic Organisms* 30: 1-9.
- MACKINNON, D.L. & ADAM, D.I. 1924. Notes on Sporozoa parasitic in *Tubifex*. I. The life-history of *Triactinomyxon* Štolc. *Quarterly Journal of Microscopical Science* 68: 187-209.
- MARQUÈS, A. 1984. Contribution à la connaissance des Actinomyxidies: ultrastructure, cycle biologique, systématique. Ph.D. thesis, Université des Sciences et Techniques du Languedoc, Montpellier, France.
- MOLNÁR, K., EL-MANSY, A. SZÉKELY, CS. & BASKA, F. 1999a. Development of *Myxobolus dispar* (Myxosporea: Myxobolidae) in an oligochaete alternate host, *Tubifex tubifex*. *Folia Parasitologica* 46: 15-21.
- 1999b. Experimental identification of the actinosporean stage of *Sphaerospora renicola* Dykova & Lom 1982 (Myxosporea: Sphaerosporidae) in oligochaete alternate hosts. *Journal of Fish Diseases* 22: 143-153.
- ÖZER, A. & WOOTTEN, R. 2000. The life cycle of *Sphaerospora truttae* (Myxozoa: Myxosporea) and some features of the biology of both the actinosporean and myxosporean stages. *Diseases of Aquatic Organisms* 40: 33-39.
- PALMER, R. 1995. Abstract. *Kudoa* in Ireland. European Association of Fish Pathologists Seventh International Conference. European Association of Fish Pathologists, England.
- PERKINS, F.O. 1990. Phylum Haplosporidia. Pp. 19-29. In Margolis, L., Corliss, J.O., Melkonian, M. & Chapman, D.J. (eds) *Handbook of Protozoa*. (Jones & Bartlett: Boston).
- POINAR, J.R., G.O. 1976. Presence of Mermithidae (Nematoda) in invertebrate paratenic hosts. *Journal of Parasitology* 62: 843-844.
1978. Associations between nematodes (Nematoda) and oligochaetes (Annelida). *Proceedings of the Helminthological Society of Washington* 45: 202-210.
- RADULESCU, I. & MOTILICA, I. 1957. Contributii la cunoasterea parazitilor Oligochetelor din Marea Neagra: *Sphaeractinomyxon stolci* Caullery-Mesnil, 1904, colectat din *Tubifex* sp. *Academia Republicii Populare Romine* 7: 953-956.
- RAFTOS, D.A. & COOPER, E.L. 1990. Diseases of Annelida. Pp. 229-243. In Kinne, O. (ed.) *Diseases of marine animals*, 3. (Biologische Anstalt Helgoland: Hamburg).
- ROUBAL, F.R., HALLETT, S.L. & LESTER, R.J.G. 1997. First record of triactinomyxon actinosporean in marine oligochaete. *Bulletin of the European Association of Fish Pathologists* 17: 83-85.
- SMITH, M.E. 1985. Naididae (Oligochaeta) as hosts for mermithid nematodes (Enoplida: Mermithidae). *Canadian Journal of Zoology* 63: 1459-1462.
- SZÉKELY, C.S., MOLNÁR, K., ESZTERBAUER, E. & BASKA, F. 1999. Experimental detection of the actinospores of *Myxobolus pseudodispar* (Myxosporea: Myxobolidae) in oligochaete alternate hosts. *Diseases of Aquatic Organisms* 38: 219-224.
- USPENSKAYA, A.V. 1995. Alternation of actinosporean and myxosporean phases in the life cycle of *Zschokkella nova* (Myxozoa). *Journal of Eukaryotic Microbiology* 42: 665-668.
- WEISER, J. 1985. Phylum Myxozoa Grassé, 1970. Pp. 384-392. In Lee, J.J., Hutner, S.H. & Bovee, E.L. (eds) *Illustrated guide to the Protozoa*. (Society of Protozoologists: Kansas).
- WOLF, K., MARKIW, M.E. & HILTUNEN, J.K. 1986. Salmonid whirling disease: *Tubifex tubifex* (Müller) identified as the essential oligochaete in the protozoan life cycle. *Journal of Fish Diseases* 9: 83-85.
- XIAO, C. & DESSER, S.S. 1998a. Actinosporean stages of Myxozoan parasites of oligochaetes from Lake Sasajewun, Algonquin Park, Ontario: new forms of triactinomyxon and raabeia. *Journal of Parasitology* 84: 998-1009.
- 1998b. Actinosporean stages of Myxozoan parasites of oligochaetes from Lake Sasajewun, Algonquin Park, Ontario: new forms of echinactomyxon, neoactinomyxon, aurantiactinomyxon, guyenotia, synactinomyxon and antonactinomyxon. *Journal of Parasitology* 84: 1010-1019.
- 1998c. The oligochaetes and their actinosporean parasites in Lake Sasajewun, Algonquin Park, Ontario. *Journal of Parasitology* 84: 1010-1019.
- YOKOYAMA, H., OGAWA, K. & WAKABAYASHI, H. 1991. A new collection method of actinosporeans - a probable infective stage of myxosporeans to fishes - from tubificids and experimental infection of goldfish with the actinosporean, *Raabeia* sp. *Gyobyo Kenkyu* 26: 133-138.
- 1993a. Involvement of *Branchiura sowerbyi* (Oligochaeta: Annelida) in the transmission of *Hoferellus carassii* (Myxosporea: Myxozoa), the causative agent of kidney enlargement disease (KED) of goldfish *Carassius auratus*. *Gyobyo Kenkyu* 28: 135-139.
- 1993b. Some biological characteristics of actinosporeans from the oligochaete *Branchiura sowerbyi*. *Diseases of Aquatic Organisms* 17: 223-228.

THE 'WATER-TRAP' SPINY OYSTER, *SPONDYLUS VARIUS* G.B. SOWERBY I, 1827
(MOLLUSCA: BIVALVIA: SPONDYLIDAE) FROM AUSTRALIA

JOHN M. HEALY, KEVIN LAMPRELL AND JENNIFER L. KEYS

Healy, J.M., Lamprell, K. & Keys, J.L., 2001 06 30: The 'water-trap' spiny oyster, *Spondylus varius* G.B. Sowerby I, 1827 (Mollusca: Bivalvia: Spondylidae) from Australia. *Memoirs of the Queensland Museum* 46(2): 577-588. Brisbane. ISSN 0079-8835.

Spondylus varius G.B. Sowerby I, 1827, the largest member of the pectinoidean family Spondylidae, is recorded for the first time from Australian waters. Previously known from the Philippines, the Solomons and New Caledonia, it is now recorded from Orpheus and Lizard Islands in northern Queensland. A neotype is established for *S. varius* because: 1) no type material appears ever to have been deposited and no illustrations accompany Sowerby's original description; 2) validity of the species has been questioned; 3) juveniles of *S. varius* can potentially be confused with other species of *Spondylus* (especially *S. echinatus* and *S. castus*). Aside from its exceptionally large size (rv height up to 400mm), *S. varius* is also unique among the Spondylidae in often producing water/gas-filled chambers (defined by thin, shell septa) in one or both of the valves in mature specimens (> 100mm, sometimes occurring in subadult specimens) especially those living in coral overhangs or threatened by epibiont smothering. These chambers possibly play a role in maintaining the position of the animal in relation to the shell margin, thereby optimising water current flow (and therefore feeding and respiration). Given the extremely odorous quality of the enclosed liquid (an acidic, saline solution) the chambers could also act as a last resort deterrent to predation. A total of 55 species of Spondylidae are now recorded from Australia. □ *Spondylidae*, *Pectinoidea*, *spiny oysters*, *bivalves*, *Australian fauna*, *new record*, *neotype*.

John M. Healy and Jennifer Keys, Department of Zoology and Entomology, University of Queensland, St Lucia 4072 (e-mail: jhealy@zoology.uq.edu.au; jkeys@zoology.uq.edu.au); Kevin Lamprell, Queensland Museum, PO Box 3300, South Brisbane, 4101, Australia (e-mail: k.lamprell@uq.net.au); 14 April 2000

The waters around the Australian coastline are prolific in bivalve molluscs but especially so in tropical and subtropical areas which share several species with adjacent regions of the Indo-Pacific (Lamprell & Whitehead, 1992; Lamprell & Healy, 1998). Featuring prominently within the Australian molluscan fauna are the Spondylidae ('spiny oysters'), with 54 previously recorded species (Lamprell & Healy, 1998). Although several species are known from the southern states, including some endemics (Lamprell, 1992), the Spondylidae are more speciose off the subtropical to northern Australian coastline.

During November 1998, one of us (JK) collected a very large spondylid from shallow water off Orpheus Island, northern Queensland. After cleaning and close inspection, the species was determined as *Spondylus varius* G.B. Sowerby I, 1827 — a new record for the Australian bivalve fauna. A subsequent search of the collections of the Australian Museum (Sydney) revealed other specimens of this species. *Spondylus varius* is probably the largest spondylid to have ever existed, reaching a

maximum of 400mm in shell height (umbones to ventral margin — measurement based on in situ measurements of Solomon Islands specimens, P. Clarkson, pers. comm.). Only the tropical Atlantic species *S. limbatus* G.B. Sowerby II, 1897, rivals the dimensions of *S. varius* (up to 267mm maximum height according to Eisenberg (1981)). Together with the giant clams (Tridacnidae) and pen shells (Pinnidae), *S. varius* and *S. limbatus* rank among the largest of the extant Bivalvia. In addition to its exceptionally large size, *S. varius* is also unique among the Spondylidae for its habit of often producing fluid and gas-filled chambers sometimes referred to as 'water-traps' (Lamprell, 1986) in one or both valves. This phenomenon was investigated by Sir Richard Owen (1837, 1838) who concluded that chamber production in *S. varius* was probably a response of the animal to overgrowth from encrusting life such as corals.

Juvenile *S. varius* differ from adults in colour and, usually, in the absence of water-filled chambers, leading to difficulty in identifying immature specimens and confusion with other species such as *S. echinatus* Schreibers, 1793 and

S. castus Reeve, 1856. Tomlin (1937: 350) considered Sowerby's (1827b) original description as vague and possibly based on material of more than one species.

The purposes of the present account are to: 1) record *Spondylus varius* in Australian waters; 2) establish a neotype; 3) clarify the publication date; 4) provide a revised diagnosis based on material from the entire known range and 5) discuss possible functions of the fluid and gas-filled chambers.

MATERIAL AND METHODS

The living specimen of *Spondylus varius* G.B. Sowerby I, 1827 was collected at depth of 10m, attached to a slight coral overhang, off the point between Pioneer Bay and Hazard Bay, Orpheus Island (18°36'S, 146°29'E) during November, 1998. The specimen was photographed in the aquarium at the Orpheus Island Research Station to record the distinctive mantle pattern. After removal of the animal (for later gonad studies) the shell was partially cleaned of excessive coral encrustations by overnight immersion in 10% w/v sodium hypochlorite solution. The shell is now deposited at the Queensland Museum (QMMO67048). For comparison with the Australian specimen, material from the Solomon Islands and the Philippines (all Lamprell Collection), and the Natural History Museum (London) (the specimen figured by G.B. Sowerby II (1847) and Reeve (1856)) are also figured. Height measurements are from umbones to ventral margin; width measurements are from anterior to posterior margins.

Abbreviations: AMSC = Australian Museum, Sydney; BMNH = Natural History Museum, London; I = Island; KL = Lamprell Collection; lv = left (or top) valve; pv = paired or conjoined valves; Qld = Queensland; rv = right (or lower) valve.

SYSTEMATICS

FAMILY SPONDYLIDAE Gray, 1826

Spondylus Linnaeus, 1758.

TYPE SPECIES. *Spondylus guederopus* Linnaeus, 1758, by subsequent designation of Schmidt, 1818: 61.

Spondylus varius G.B. Sowerby I, 1827 (Figs 1-6)

Spondylus varius Sowerby, 1827; G.B. Sowerby I, 1827b: 1-2; Tomlin, 1937: 350; 1943: 143.

Spondylus varius Sowerby, 1829; [sic] Fulton, 1915: 358, sp. 71; Lamprell, 1986: 68, pl. 25, fig. 2.

Spondylus varians Sowerby, [sic, no date specified]; G.B. Sowerby II, 1847: 426, pl. 86, figs 21, 22; Reeve, 1856: sp. 3, pl. 1, fig. 3; Hanley 1842-56: 293

Spondylus varians Sowerby, 1829 [sic]; Springsteen & Leobrera 1986: 325, pl. 92, fig. 16.

Spondylus delessertii Chenu, 1845: 5.

TYPE LOCALITY. Not stated by Sowerby (1827b); type locality of neotype (here designated; specimen BMNH 1952.10.30.3): 'Pacific Islands' (locality as stated on label).

TYPE MATERIAL. NEOTYPE (here designated; Figs 1A-E, 6B): 1 pv BMNH 1952.10.30.3, 'Pacific Islands' (locality as stated on label). Figured by Sowerby, 1847, pl. 86, fig. 21 and Reeve, 1856, pl. 1, sp. 3. Dimensions of neotype (excluding spines): lv height 154mm, width 137mm; rv height 169mm, width 140mm; pv height 169mm, width 140mm, depth 70mm; (measurements including spines) - lv height 163mm, width 143mm; rv height 174mm, width 155mm, pv height 179mm, width 155mm, depth 75mm.

OTHER MATERIAL. (all measurements excluding spines; Table 1) AUSTRALIA: AMSC104588 Watson Bay, Lizard I., Qld, 14°40'S, 145°27'E, 2.5m among corals and sand lv height 195mm, rv height 255mm, pv depth 100mm; AMSC150016 Orpheus I., Qld, 18°36'S, 146°29'E, 10m base of bommie, 1pv, lv height 155mm, rv height 200mm, pv depth 80mm, water chambers on lv; 1pv QMMO67048 approximately 10 m depth attached to a slight coral overhang off the point between Pioneer Bay and Hazard Bay, Orpheus I., Qld, 18°37'S, 146°30'E, rv height 170mm, lv height 138mm, pv depth 94mm, water chambers in both valves (see Figs 2A-D, 3A,B). NEW CALEDONIA: AMSC100790 Noumea, ex-aquarium, lv height 175mm, rv height 220mm, pv depth 90mm, water chamber on lv; one rv with water chamber (no data); Sud nouvelle Calédonie 2pv Grotte Merlet, 22°42.4'S, 166°41.2'E, 20-30 m, 21.1.1993, lv height 190mm (for figures see Lamprell & Healy, 2000). SOLOMON ISLANDS: AMSC303014, 1 pv, off Bonegi I shipwreck (lv height 115mm, rv height 135mm, pv depth 80mm, water chambers in both valves) (specimen figured by Lamprell, 1986); KL, 4 pv, off Bonegi I. shipwreck, 43m: spec 1 lv height 85mm, rv height 93.2 small water chamber in lv; spec 2 lv height 62mm, rv height 72.2mm, large water chamber in lv; spec. 3 lv height 56mm, rv height 65mm, water chamber in lv; spec. 4 lv height 36mm, rv height 42mm, water chambers absent (Fig. 3C,F); PHILIPPINES: KL, off Cebu I., spec 1 lv height 94mm, rv height 113mm, water chambers absent; spec 2 lv height 99mm, rv height 113mm, water chambers in both valves (Fig. 3D,E); NO DATA: KL, ex Rombouts collection, 1 pv, no locality data lv height 210mm, rv height 240mm, water chamber (empty) in both valves (senescent specimen; Fig. 5A-C).

DIAGNOSIS. Shell height of pv to 400mm; elongate-ovate; inequivalve, top valve (lv) usually depressed to slightly inflated; lower (rv) appreciably deeper than lv. Sculpture of lv with numerous, low, irregular, radial ribs ornamented with dense, slightly flattened, raised or depressed

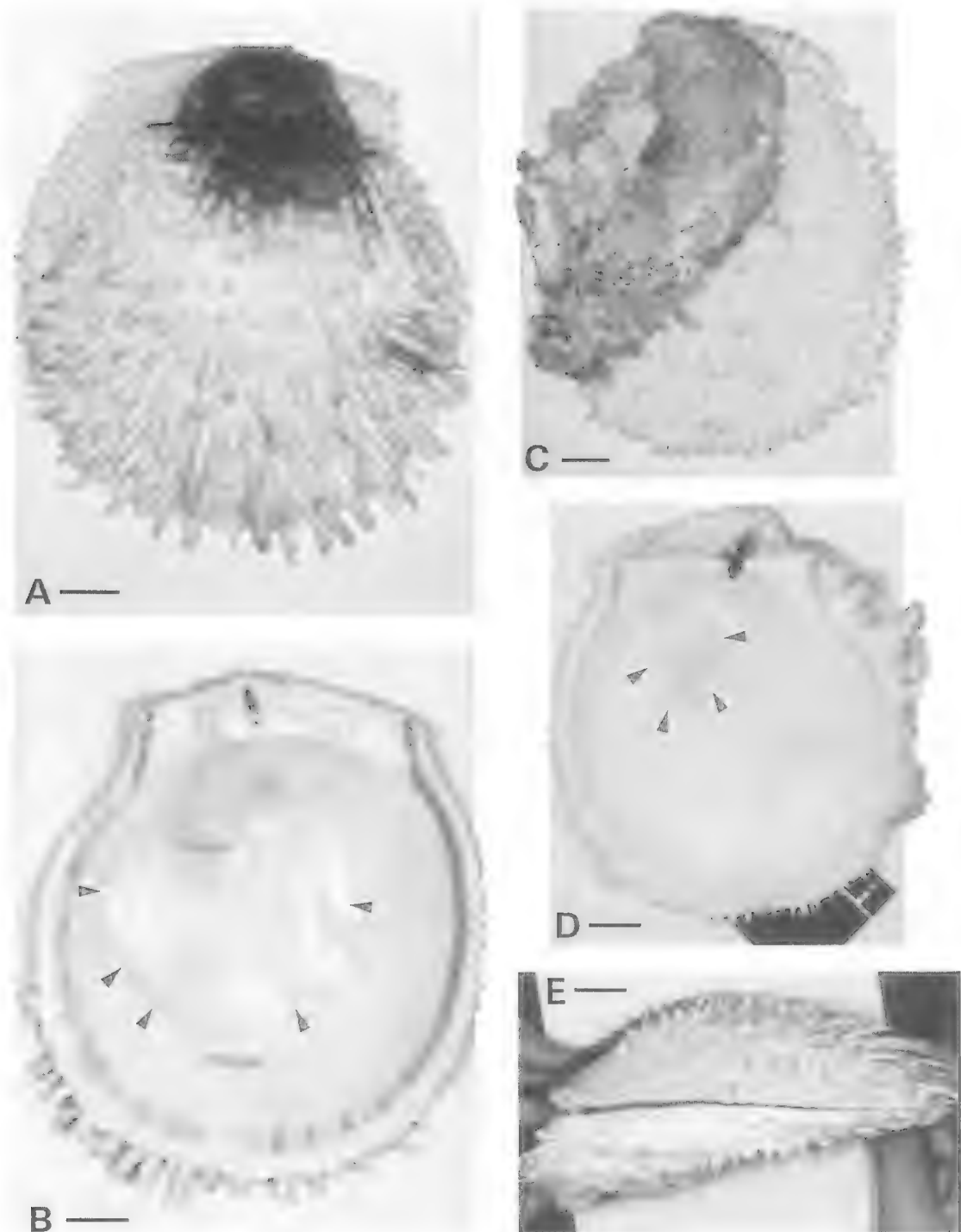


FIG. 1. *Spondylus varius* Sowerby, 1827. Neotype (here designated) 1 pv BMNH 1952.10.30.3, 'Pacific Islands' (locality as stated on labels). Figured by G.B. Sowerby II, (1847) in the *Thesaurus Conchyliorum*: pl. 86, fig. 21 (see Fig. 6B herein) and Reeve, (1856) in the *Conchologia Iconica*: pl. 1, sp. 3. A, External view of lv. B, Internal view of lv showing visible (but empty) water chamber (arrow heads). C, External view of rv. D, Internal view of rv showing visible (but empty) water chamber (arrow heads). E, Profile view of pv. Scale bars = 20mm.

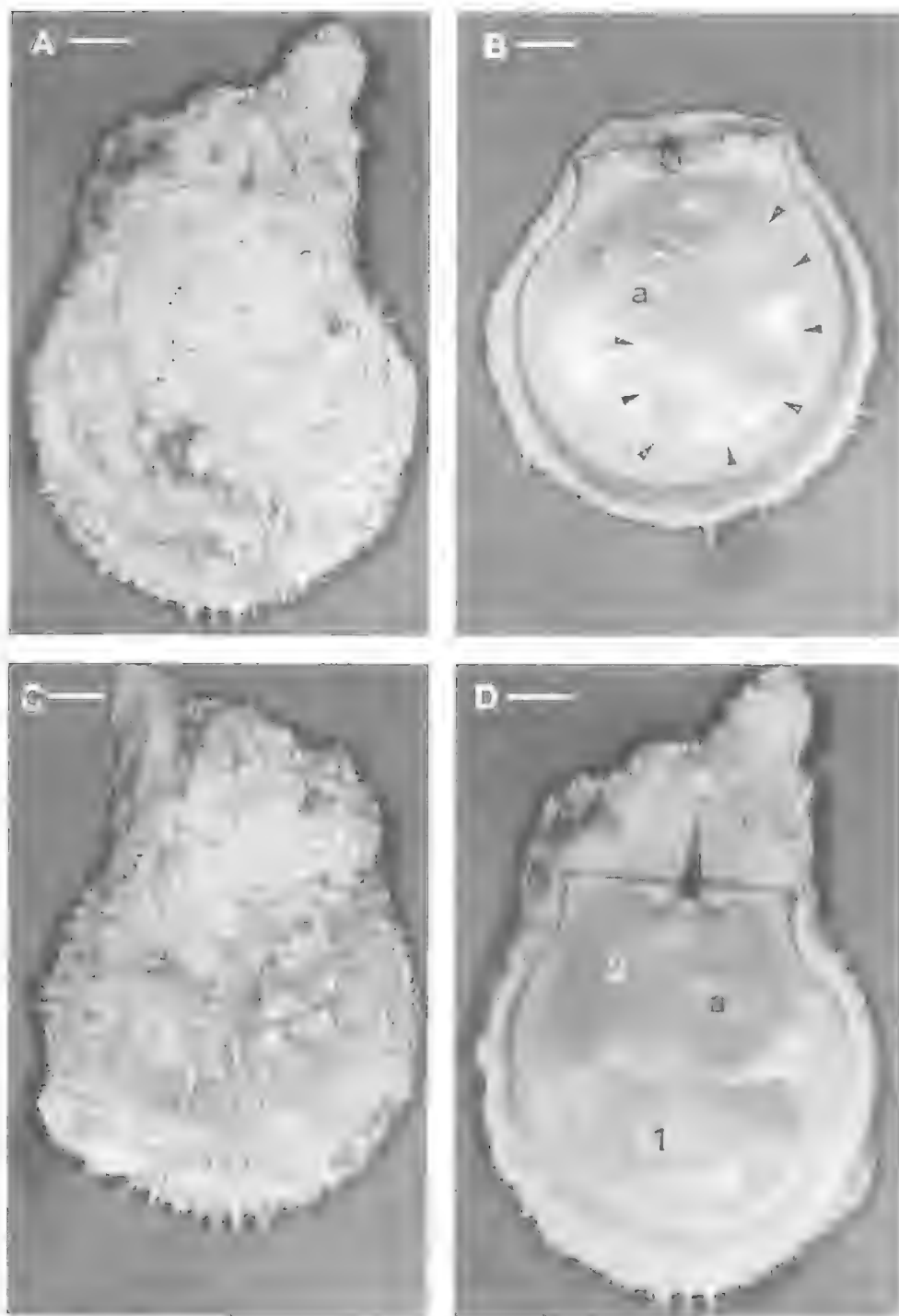


FIG. 2. *Spondylus varius* Sowerby, 1827. A-D, Specimen from 10m, between Pioneer Bay and Hazard Bay, Orpheus I., Queensland, 18°37'S, 146°30'E (QMMO67048). A, External view of pv from aspect of lv. B, Internal view of rv showing the visible water chamber (arrow heads). C, External view of pv from aspect of rv. D, Internal view of rv showing two visible water chambers. Note broken uppermost water chamber overlying most of lower (intact) water chamber (the latter indicated by arrow heads). Scale bars = 20mm.

ribs in juvenile specimens (< 100mm rv height), becoming longer towards ventral margin. In mature specimens (100-400mm rv height) spines sometimes long but usually short, blunt and appressed (extremely stunted in specimens over 200mm rv height); interstices in uneroded specimens have fine, dense appressed spines. Rv with similar radial ribs to those of lv; ornamentation of foliations extending out from umbonal (fixation) area; remainder of rv similarly spined to lv. Hinge line broad, straight, showing typical spondylid dentition of two, large, isodont teeth on rv, fitting into sockets on lv; ligament and ligament pit between teeth/sockets. Auricles broad. Externally, shell usually white, almost always with a clearly defined orange-red-purple area umbonally which occasionally extends into the spines or over entire shell length (especially in small juveniles < 50mm rv height). Internally, glossy white with yellow-orange margin. Radiating ribs visible internally, stronger marginally forming a strong, wide crenulated margin. Mature and senescent specimens (height of rv 100-400mm, excluding spines) often exhibiting fluid and gas-filled, vertically-stacked chambers within one or both valves. Chamber septa composed of smooth, translucent shell, associated with or completely surrounding the adductor scar (rarely passing partially under scar). Chambers sometimes also occurring in juveniles (of rv height 60-80mm, excluding spines) but absent in smaller specimens (rv height < 60mm). Fluid from chambers usually lost through evaporation over an extended period of dry storage (or rapidly if septum is cracked). Table 1 lists the incidence of externally detectable water chambers in material examined herein. For material <100mm in shell height the absence of chambers represents a verifiable absence of these structures, whereas in thicker, more mature specimens, the absence of visible, surface chambers (that is, ones which are fluid/gas-filled in fresh material) in one or both valves does not necessarily preclude the presence of one or more lower (empty) chambers.

OBSERVATIONS ON LIVE-COLLECTED SPECIMENS. The live-collected specimen from Orpheus I. (Figs 1A-D, 2A-D, 3A,B, 4A,B) has lv 170mm in height, and 130mm in width (from anterior to posterior margin in the lv). Although considerably encrusted with calcareous material, treatment with commercial hydrochloric acid soon revealed the external colour to be white with some traces of red-purple umbonally. The rv contains two visible water chambers, one

overlying the other (Figs 2B,D, 4A,B) whereas the lv exhibits only a single visible chamber. The presence of fluid within the chambers is clearly indicated by the large gas bubbles which move around when the shell is tilted. During the initial stage of shell cleaning after removal of the animal, the uppermost of the two water chambers lining the inside of the rv was accidentally broken, thereby allowing release of the clear, faintly yellowish fluid contents. This fluid was slightly more viscous than water and extremely foul-smelling (? partly due to the gas within the traps) — both characteristics suggesting decomposing proteinaceous material. The septum of the broken chamber consists of translucent-white, glossy, shell material and has a thickness of approximately 0.3mm (lamella thickness). Internally both valves are white with the exception of the crenulated, brown-purple margins and the regions associated with the water chambers which appear brownish owing to the discoloured fluid contained therein.

Live *Spondylus varius* has an extensive and gaping mantle which exhibits large, irregularly-shaped mottlings (Fig. 3B; white on a black background in Orpheus I. specimen, this study; orange on green background in Solomon Islands specimens, P. Clarkson, pers. comm.; white on yellow background (Slack-Smith, 1998, pl. 12.5). Variation in mantle colour is possibly associated with age, sex of the animal or represents some degree of geographical variation. Edges of the mantle are red-orange in colour and ornamented with numerous blue ocelli. The ocelli are associated with rapid closure of the valves during disturbances including the approach of a diver. Large specimens of *S. varius* may weigh several kilograms, and live to be at least ten years of age (P. Clarkson, pers. comm.).

HABITAT AND DISTRIBUTION. *Spondylus varius* is usually found cemented umbonally to gently sloping reefs, vertical drop-offs, shipwrecks and concrete pylons, in depths from 3m to more than 60m water in prominent positions exposed to nutrient laden currents. Specimens with particularly well-developed spines occur in sheltered positions within shipwrecks, where they are attached to a variety of surfaces and obscured by silt or sponges rather than calcareous encrusting organisms. They commonly provide habitat for other molluscs, including other cemented bivalves (other Spondylidae, Chamidae, Ostreoidea) and gastropods such as cowries and muricids. *S.*

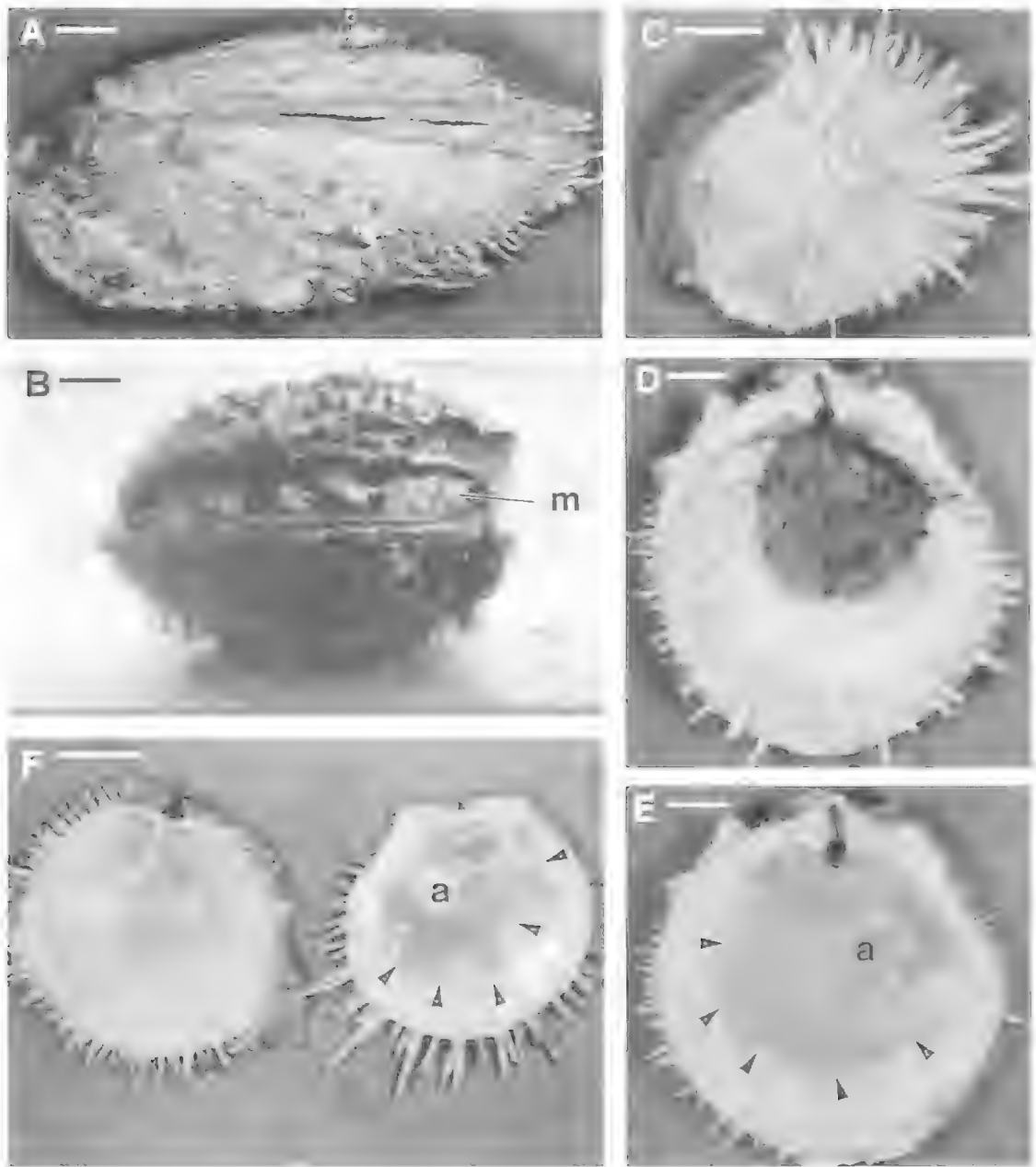


FIG. 3. *Spondylus varius* Sowerby, 1827. A, Profile of pv from 10m, between Pioneer and Hazard Bays, Orpheus I., Queensland (QMMO 67048). B, Same specimen photographed alive in aquarium at Orpheus I. Research Station. Clearly visible is the black and white mottled mantle. C, Pv of juvenile from 43m off, Bonegi Island wrecks, Solomon Islands showing long spines (KL). D, External of lv of juvenile specimen from off Cebu I., Philippines — note darker shell colour (purple in this case) of younger portion of shell (KL). E, Rv of same specimen as Fig. 3D showing water chamber (arrow heads). F, Internal views of left valve (at right) and right valve (at left) of juvenile specimen from 43m, off Bonegi I. wrecks, Solomon Islands, showing water chamber in lv (KL). Scale bars = 20mm.

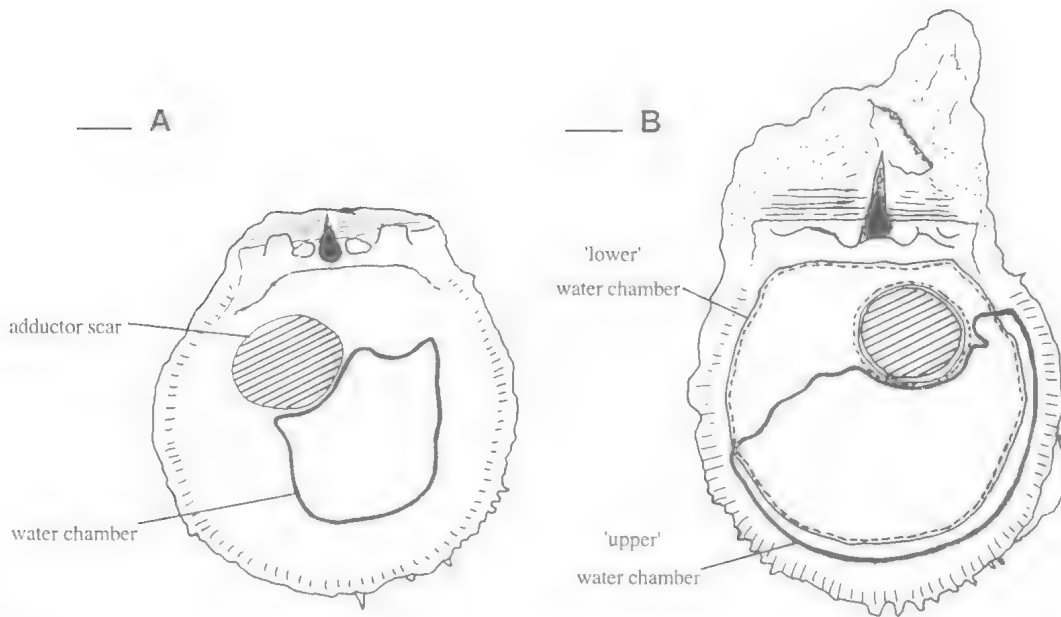


FIG. 4. *Spondylus varius* Sowerby, 1827. Sketches showing extent of the water chambers (dotted lines) in QM MO67048. A, Lv; B, Rv – note two visible water chambers, the upper one broken. Scale bars = 20mm.

varius is recorded from the Philippines (Lamprell, 1986; Springsteen & Leobrera, 1986), Solomon Islands (Lamprell, 1986), northern Queensland and New Caledonia (Lamprell & Healy, 2001). The species has yet to be taken in the eastern Pacific, and we know of no Hawaiian records.

DISCUSSION. *General remarks and comparisons.* This is the first published record of this large and unusual bivalve from Australian waters, bringing the number of spondylid species known to occur in the region to 55. Sowerby (1827b) offered no precise locality data for *S. varius* other than to say that the material offered in the auction catalogue were 'shells collected by Mr. Samuel Stutchbury on the coast of some islands of the Australian and Polynesian groups'. Tomlin (1943) located a complete copy of the Sowerby auction catalogue which records in one annotation that catalogue specimens of *S. varius* were from 'Bow Island' ('one of the Paumotu group according to Tomlin (1943) = Hao Atoll, Archipel des Tuamotu, 9°22'S, 171°14, French Polynesia). Although we have not examined material from French Polynesia, there is no compelling reason to believe that *S. varius* does not occur there (possibly all of Stutchbury's material was collected at 'Bow Island'). Reeve (1856) gave the collection locality of the Cuming

Collection specimen (designated herein as the neotype of *S. varius*) as 'Pacific Islands'.

Possibly because of its preference for semi-secluded habitats such as sunken ships or coral overhang, *S. varius* may have been observed previously by divers in Australian waters but not identified as such. Specimens of *S. varius* were also found in the collections of the Australian Museum, but somehow these have remained overlooked and undocumented until now. The exceptionally large size reached by *S. varius* (maximum height 400mm — measurement based on in situ measurements of Solomon Islands specimens — P. Clarkson, pers. comm.) could have precluded collection of specimens prior to this study as divers are generally hesitant to collect or even disturb large, attached molluscs such as these. The measurement of 450mm quoted by Lamprell & Healy (1998) for the Spondylidae (not stated by them but indirectly alluding to *S. varius*) was based on anecdotal sources only. While diving on the reefs between Pioneer and Hazard Bays at Orpheus Island, one of us (JK) noted very large spondylids (estimated pv height of 250+ mm) in the vicinity of the *S. varius* specimen collected for this study. Almost certainly these were additional specimens of *S. varius* because no other spondylid occurring in the Western Pacific reaches this size.

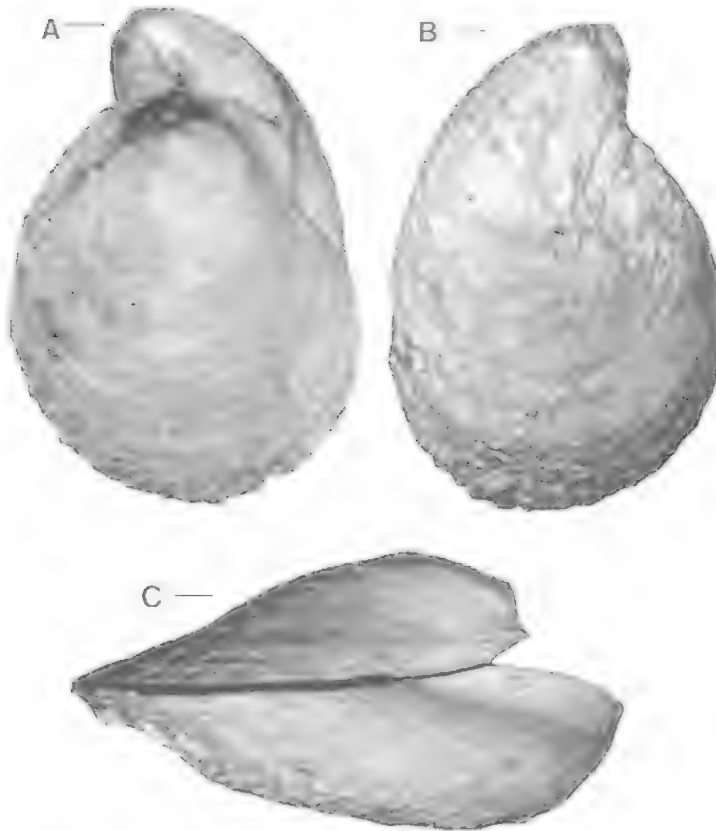


FIG. 5. *Spondylus varius* Sowerby, 1827. A-C, Aged specimen showing stunted nature of spines (KL; no locality data), height from umbones to ventral margin 257mm; A, External view of pv from lv aspect; B, External view of pv from rv aspect; C, Lateral view of pv. Scale bars = 20mm.

In its juvenile state (and before any water chambers have developed), *S. varius* can potentially be confused with *S. echinatus* Schreibers, 1793 and *S. castus* Reeve, 1856. However, *S. varius* can usually be distinguished from these species by its umbonal colouration (white, or often orange-red-purple in *S. varius*; white with black speckling in *S. echinatus* and *S. castus*). *Spondylus wrightianus* Crosse, 1872 and *S. tenuitas* Garrard, 1966 also exhibit orange-red umbonal colouration like *S. varius*, but the former is smaller, solid and equivalved and the latter is a relatively small (65mm length), equivalved temperate Australian species with delicate spines.

A review of the Spondylidae from New Caledonia (Lamprell & Healy, 2001) uncovered several new species and a significant number of species previously unrecorded from that region

including *S. varius*. It is therefore not surprising that *S. varius* should also occur on the Great Barrier Reef, and indeed it is likely that other Indo-West Pacific spondylids known from the Solomon Islands and New Caledonia will eventually be recorded from Queensland.

Taxonomic history of Spondylus varius. Confusion concerning the date of publication of the description of *Spondylus varius* stems from the fact that Sowerby I chose to publish this text in an appendix to the auction catalogue of Samuel Stutchbury's collection (principally of Polynesian shells and artefacts). Tomlin (1937) located incomplete copies of the catalogue, each with the date 'July 1827' added to a MS version of the missing title page and noted the discrepancy between this date and the tentative date '? 1829' written on the Natural History Museum's (then only) copy of the catalogue. Later a complete copy of the catalogue was sighted by Tomlin (1943) allowing him to clarify the date of the auction as July 26th, 1827. Tomlin concluded that this complete copy of the catalogue was probably Stutchbury's, for it is

annotated and bound into the back of a copy of J.G. Children's *Lamarek's Genera of Shells* bearing Stutchbury's signature). Although it is impossible to state the exact date of publication of the auction catalogue, it seems almost certain that this occurred in the first few months of 1827, and not in 1826. For some reason, however, the year 1829 has regularly been associated with the name *Spondylus varius* Sowerby and, at present, the labels of the Natural History Museum specimen figured by G.B. Sowerby II (1847) and Reeve (1856) still bear the date 1829. Fulton (1915) appears to be the first author to cite 1829 as the authority year for *S. varius* Sowerby. Conceivably however, the first usage of this erroneous date may have been earlier than 1915, perhaps arising in dealers' listings and subsequently repeated by Fulton.

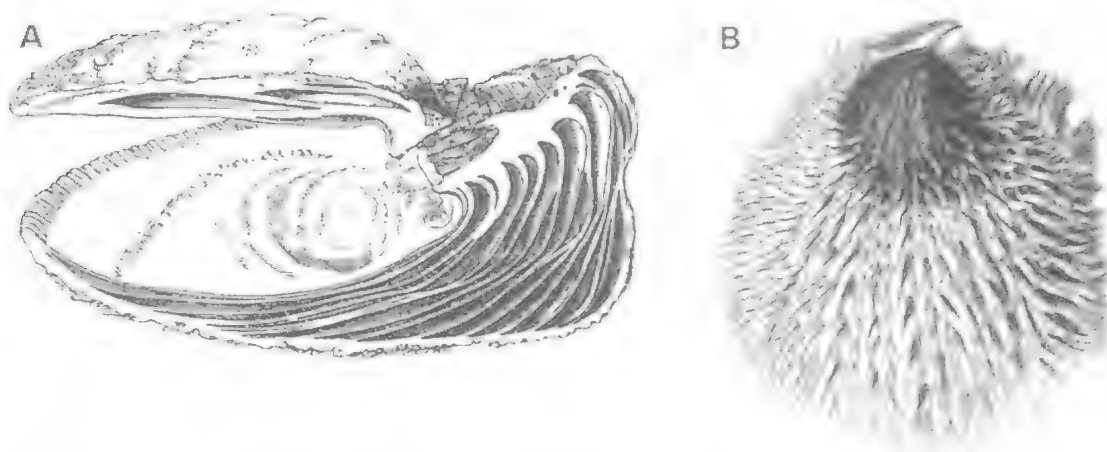


FIG. 6. *Spondylus varius* Sowerby, 1827. A, Illustration from Owen (1838, fig. 21) of a longitudinal section through pv of *S. varius* showing the multiple, vertically stacked, slightly offset septa of water chambers (note bifurcation of each septum into two lamellate layers). B, Illustration from Sowerby (1847, fig. 21, pl. 86) of *S. varius* here chosen as neotype (BMNH 1952.10.30.3): external view of pv from aspect of rv.

To our knowledge, alteration of the name *S. varius* to *S. varians* was first made by Sowerby (1847) and unaccompanied by any explanation. This name change appears deliberate and not a *lapsus calami* as it occurs not only in Sowerby's (1847) main text but also in his List of Figures and Alphabetical Index.

Tomlin (1937: 350) considered the original description of *S. varius* (Sowerby, 1827) to be 'rather vague, and one rather suspects that it may have been taken from a series comprising more than one species'. Undoubtedly this view was influenced not only by Sowerby's choice of name (*varius*) but also his admission that 'Under all other circumstances their form is exceedingly varied' (Sowerby, 1827b: 2). Sowerby (1827a, b) did not illustrate *S. varius* nor did he mention deposition of any type material. It is clear from Sowerby's original description that he was familiar with his new species outside of the series of specimens included in the auction ('Many of the specimens of this shell are extremely beautiful, and there is in the Sale an interesting series of specimens of different sizes and variously circumstanced', Sowerby, 1827b: 2). The neotype, figured by Sowerby (1847, pl. 86, fig. 21) and Reeve (1856, pl. 1, fig. 3.) (BMNH 1952.10.30.3.), has obvious historical significance, but to our knowledge, there is no surviving documentation to prove that it originated from the material offered in the auction catalogue or from other material used by Sowerby in his 1827 description (or from material collected after 1827). Associated with

this specimen in the Natural History Museum is a note stating that it has no type status. Reeve (1856) referred to this shell as being from Cuming's collection ('Cuming Mus.') but as to the ultimate source of this specimen nothing is known, other than it was collected in the 'Pacific Islands'.

Our reasons for nominating BMNH 1952.10.30.3. as neotype are: 1) this shell was accepted both by G.B. Sowerby II (1847) and Reeve (1856) (and presumably also Sowerby I who died in 1854), as characterising the species, and is accurately illustrated in colour by both authors; 2) the specimen is in an excellent state of preservation, even though the liquid contents of the water chambers have been lost through gradual evaporation; 3) the locality data associated with this specimen ('Pacific Islands') reasonably accurately reflects the known distribution of *S. varius*, although the species has yet to be collected from the eastern Pacific or the Indian Ocean. Nomination of a neotype is here deemed necessary to eliminate any doubts concerning the validity of *S. varius* (e.g. Tomlin's (1937) comment that the species may have been based on specimens of more than one species).

Structure and possible function(s) of the water chambers. The function of the water chambers in *S. varius* remains unclear. Over 150 years ago, Sir Richard Owen investigated the structure of the fluid/gas chambers in this species in two brief, but highly informative, papers (1837, 1838). He demonstrated a sequence of 14 vertically-stacked, slightly off-set chambers (each defined

TABLE 1. Comparison of *Spondylus varius* specimens examined.

Collection Reference	Locality	Water Chambers (visible externally)	RV Height (excluding spines)	LV Height (excluding spines)
QMMO67048	Orpheus I., Qld	In both valves	170mm	138mm
AMSC150016	Orpheus I., Qld	In lv only	200mm	155mm
AMSC104588	Lizard I., Qld	In lv only	255mm	195mm
AMSC100790	New Caledonia	In lv only	220mm	175mm
AMSC303014	Solomon Is	In both valves	135mm	115mm
KL	Solomon Is	In lv only	65mm	56mm
KL	Solomon Is	In lv only	72mm	62mm
KL	Solomon Is	Chambers absent	42mm	36mm
KL	Solomon Is	In lv only	93mm	85mm
KL	Philippines	Chambers absent	113mm	94mm
KL	Philippines	In both valves	113mm	99mm
KL	No data	In both valves	240mm	210mm
BMNH 1952.10.30.3 (neotype)	Pacific Islands	In both valves	169mm	154mm

by shell septa) in the rv (lower valve) of a large specimen which he had sectioned longitudinally from umbones to ventral margin (Fig. 6A). The upper valve of his specimen contained fewer, more lenticular chambers, which Owen (1837) originally ascribed to a reduced shell-secreting capability of the lv (upper valve) mantle but later (1838) interpreted as a result of reduced demand for such a capability in this region of the mantle (that is, both the upper and lower valve mantle margins probably have equal shell-secreting abilities). Septa of the chambers in the rv were shown by Owen to bifurcate away from the attachment area of the valve, so that strictly each septum is composed of two thin lamellae for most of its length.

After discussing the phenomenon of septal production in other attached bivalves (ostreids and gryphaeids), in attached gastropods (vermetids and certain muricids) and in chambered cephalopods, Owen (1837, 1838) hypothesised that the presence of septa in *S. varius* was probably a continuing response of the animal to impending overgrowth by corals. Hence the attached animal could effectively counteract overgrowth, and therefore maintain an unimpeded water flow for respiration and filter feeding, by raising the mantle edge on a series of successive shell platforms (= the septa defining the chambers). In support of this idea, Owen (1838) cited a personal communication from Stutchbury claiming that chambers only occurred in specimens associated with coral overhangs or other situations where over-growth by corals seemed imminent. In this species, water

chambers may occur on the upper valve, the lower valve or commonly on both (Owen, 1837, 1838; Lamprell, 1986; Springsteen & Leobrera, 1986; present study), and even though it has been suggested that the fluid/gas chambers are only a feature of older specimens (Sowerby, 1827, 1848; Lamprell, 1986) we have sometimes observed them in relatively young shells (rv 72mm height) from the Solomons and the Philippines (Fig. 5C-F). We cannot definitively assess Owen's 'overgrowth' theory, but admit that his explanation is well argued and probably correct. However the chambers in some sub-adult *S. varius* — animals not as yet threatened by epibiont smothering — and the absence of such chambers in other spondylid species (including all other large species, Lamprell & Clarkson, unpubl. data), suggest that there may be additional functions for these structures. The foul-smelling odour of the fluid contained within the water chambers may offer another clue as to the function of these structures. Owen (1837, 1838) had the fluid analysed by a colleague, Dr Bostock, who reported that 'it was turbid, had an acid-saline taste, and a rank disagreeable odour'. After allowing the fluid to settle for 24 hours he determined that the clear supernatant was essentially a saline (sodium chloride) solution, with some hydrochloric acid and a little sulphuric acid also present. Dr Bostock made a point of emphasising that the fluid differed in its composition from sea water, raising the question as to its origin. If Owen's (1837, 1838) proposed sequence of events for septal secretion is accepted, then sea water seems

the most likely source of the water chamber fluid. Possibly the mantle has an ability to chemically modify the contents of the fluid immediately before it is sealed off from the environment. More likely perhaps, chemical changes occur within the water once it is enclosed resulting in the precipitation of certain dissolved salts leaving a predominantly sodium chloride solution within the water chamber. In addition to the above results Dr Bostock isolated 'a little brown matter' which he tentatively concluded 'gave the fluid its peculiar flavour and odour'. We can certainly confirm the repugnant odour of the fluid (? and gas) in *S. varius* and given this property, and the brittle nature of the septa, it is possible that fluid/gas-filled chambers may act as a last-resort defence against predators once maturity has been reached. The use of repugnatorial chemicals for defence against predators is widely recorded in the animal kingdom, although in most cases species adopting such a strategy advertise their inedibility (or even poisonous nature) through the use of bright colours and patterns (for example many nudibranchs, xanthid crabs).

ACKNOWLEDGEMENTS

We thank the Director of the Orpheus I Research Station, Mr M. Fogg, for allowing us access to the station's facilities during November, 1998. Miss N. Wilson and Mr. B. O'Kane (Department of Zoology, University of Queensland) acted as dive buddies and volunteer assistants to one of us (JK) during the course of the field work. We extend our thanks to Mrs J. Pickering and Ms K. Way (Natural History Museum, London) for providing information on the status of the specimen of *Spondylus varius* figured by Sowerby and by Reeve and for a photocopy of the 1827 auction catalogue. Mrs Pickering and Ms Way are also thanked for facilitating our access to the Natural History collections for photography of spondylid material during our visit. Dr T. Waller (Malacology Section, Smithsonian Institution) kindly checked the Smithsonian malacological collection for possible type material of *S. varius*. We also thank Mr P. Clarkson (Port Lincoln, South Australia) for sharing his observations on living *S. varius* from the Solomon Islands. The referees are thanked for their constructive comments on the original manuscript. We are especially grateful to Ms Alison Miller (Australian Museum, Sydney) and Mrs Victoria Harrison (Queensland Museum Library) for obtaining copies of some old literature. This

study was supported financially by a research grant and Senior Research Fellowship both from the Australian Research Council (to JH), a grant from the Malacological Society of Australasia (to KL) and University of Queensland Research Grants (to JH and JK).

LITERATURE CITED

- CHENU, J.C. 1845. Illustrations conchyliologiques Vol. 3. Bivalves, Part 2.
- EISENBERG, J. M. 1981. A collector's guide to seashells of the world. (McGraw-Hill Book Company: New York & Maidenhead).
- FULTON, 1915. List of the Recent species of *Spondylus* Linne with some notes and descriptions of six new forms. Journal of Conchology 14: 331-360.
- HANLEY, S. 1842-1856. An illustrated and descriptive catalogue of Recent bivalve shells. with 960 figures by Wood and Sowerby (Williams & Norgate: London).
- LAMPRELL, K. 1986. *Spondylus*, spiny oyster shells of the World. (Robert Brown & Associates: Bathurst).
1992. Notes on the genus *Spondylus* Linnaeus with descriptions of two new species from Western Australia. Memoirs of the Queensland Museum 32: 189-194.
- LAMPRELL, K. & WHITEHEAD, T. 1992. Bivalves of Australia. Vol. 1. (Crawford House Publications: Bathurst).
- LAMPRELL, K. & HEALY, J. 1998. Bivalves of Australia. Vol. 2. (Backhuys Publishers: Leiden).
2001. The Recent Spondylidae from New Caledonia and adjacent waters, with the descriptions of eight new species, and some taxonomic notes on the species *Spondylus unacanthus* (Mawe) (Mollusca, Bivalvia, Spondylidae). Bulletin du Muséum National d'Histoire Naturelle, Paris (Zoologie) 22.
- OWEN, R. 1837. Structure of water clam shell. Proceedings of the Zoological Society, 5: 63-66.
1838. Observations upon the camerated structure in the valves of the water clam (*Spondylus varius*, Sow.). Annals and Magazine of Natural History 2: 407-412.
- REEVE, L.A. 1856. Monograph on the genus *Spondylus*. Pls 1-18. In Conchologica Iconica or illustrations of the shells of molluscous Animals. Vol. 9. (Reeve: London).
- SLACK-SMITH, S.M. 1998. Ostreoida. Pp. 268-282. In Beesley, P.L., Ross, G.J.B. & A. Wells (eds) Mollusca the southern synthesis. Fauna of Australia, Vol. 5 Part A. (CSIRO Publishing: Melbourne).
- SOWERBY, G.B. 1 1827a. Catalogue of the whole of that splendid collection of rare shells, madrepores, carved paddles and other curiosities formed by Mr Samuel Stutchbury (principally among the Polynesian group of the south seas) and brought home by the Pacific Pearl Company's ship the Sir George Osbourne. [Shell sale catalogue;

authorship almost certainly G.B. Sowerby I, the auctioneer; catalogue printed sometime prior to the auction date, July 26, 1827, but presumably within the early months of 1827). Pp 1-10, plus two pages with hand-written notes (one identifying the copy as belonging to Stutchbury and one giving locality data for three species, including *Spondylus varius*]

1827b. Observations on a few of the most remarkable shells collected by Mr. Samuel Stutchbury on the coast of some of the islands of the Australasian and Polynesian groups, together with descriptions of a few new species. Appendix

to July 26th, 1827 Sales Catalogue, pp 1-4 with 1 plate.

SOWERBY, G.B. II 1847. Thesaurus Conchyliorum Vol. 1. Pp. 417-433, pls 84-89. (Sowerby: London).

SPRINGSTEEN, F.J. & LEOBRERA, F.M. 1986. Shells of the Philippines. (Carfel Shell Museum: Manila).

TOMLIN, J.R. Le B. 1937. Book notes. 6. Stutchbury's catalogue. Proceedings of the Malacological Society of London 22: 350.

1943. Book notes. Addendum to book note no. 6. Stutchbury's catalogue. Proceedings of the Malacological Society of London, 25: 143.

SIX SPECIES OF MEGASCOLECINAE (MEGASCOLECIDAE: OLIGOCHAETA) FROM NEW SOUTH WALES AND THE AUSTRALIAN CAPITAL TERRITORY

B.G.M. JAMIESON

Jamieson, B.G.M. 2001 06 30: Six species of Megascolecinae (Megascolecidae: Oligochaeta) from New South Wales and the Australian Capital Territory. *Memoirs of the Queensland Museum* 46(2): 589-602. Brisbane. ISSN 0079-8835.

A small collection of earthworms from New South Wales and the Australian Capital Territory which are the subject of agricultural studies is shown to consist of five species: *Notoscolex bakeri* sp. nov.; *Spenceriella bywongensis* sp. nov.; *S. hamiltoni* (Fletcher, 1887), *S. macleayi* (Fletcher, 1889) and *S. nevellensis* sp. nov. *Notoscolex sensu stricto* is known from New South Wales and Victoria, with one species, doubtfully included, from south-western Australia. *N. bakeri* appears to be the closest known relative of *N. montiskosciuskoi* Jamieson, 1973, but differs from the latter in lacking calciferous glands. *Spenceriella* occurs in the Kosciusko Division and Darling Basin province of Australia, Lord Howe Island, and Norfolk Island. *S. macleayi* (Fletcher), *S. bywongensis* and *S. nevellensis* spp. nov., all with two pairs of spermathecae, appear closely related but differ, among other respects, in having respectively two, three and four pairs of calciferous glands. *S. hamiltoni*, with three pairs of spermathecae and of calciferous glands, is considered to be the senior synonym of *Anisochaeta chani* Blakemore, 2000. Material from the Upper Manning River, New South Wales, previously referred to *S. raymondiana* (Fletcher 1887) is distinguished as *Spenceriella manningi* sp. nov. □ *Notoscolex*, *Spenceriella*, new species, *Megascolecinae*.

B.G.M. Jamieson, Zoology Department, University of Queensland, Brisbane 4072, Australia; received 11 May 2001.

A collection of earthworms from New South Wales and the Australian Capital Territory which are the subject of agricultural studies by Geoffrey Baker, C.S.I.R.O. Entomology, is shown in the present paper to consist of: *Notoscolex bakeri* sp. nov.; *Spenceriella bywongensis* sp. nov.; *S. hamiltoni* (Fletcher, 1887), *S. macleayi* (Fletcher, 1889) and *S. nevellensis* sp. nov. In addition, material from the Upper Manning River, New South Wales, previously referred (Jamieson, 2000) to *S. raymondiana* Fletcher (1887) is distinguished as *Spenceriella manningi* sp. nov.

Notoscolex Fletcher, 1886
emend Jamieson, 2000

Notoscolex Fletcher, 1886a: 546.
Notoscolex(emend.); Jamieson, 2000: 858-860.

DIAGNOSIS. Setae 8 per segment. Combined ♂ and prostatic porophores a pair on XVIII. A single gizzard, in V and/or VI. Meronephric, with exonephric stomate nephridium median to exonephric astomate micromeronephridia caudally (the notoscolecine condition). Prostates racemose, exceptionally tubuloracemose.

REMARKS. *Notoscolex* occurs in NSW and Victoria; one species, doubtfully included, from SW Western Australia. The genus contains some species which form what is undoubtedly a

monophyletic core and other species which can, with varying confidence, be associated with or placed in this monophylum. Members of the core (*Notoscolex s. s.*, including the type-species *N. camdenensis* Fletcher, 1886a) are associated, *inter alia*, by 3 pairs of extramural calciferous glands, in XIV-XVI, a clear synapomorphy (Jamieson, 2000). Calciferous glands are absent in *N. bakeri* but it nevertheless shows close similarities to *N. montiskosciuskoi* which has 3 pairs of calciferous glands, albeit in X-XII.

Notoscolex bakeri sp. nov.
(Figs 1, 2)

MATERIAL EXAMINED. HOLOTYPE QMG218232. PARATYPES QMG218233-218234. All from N.S.W., 36°10'S, 149°20'E., in a black basaltic soil on a flat near Rock Flat Creek, 'Rosebrook' approx. 14 km NE of Cooma, L. Robinson; 3 macerated clitellate specimens.

DESCRIPTION. Length 225 (P2), 250 (P1), >255mm (H). Width (midclitellar) 8mm (H, P1,2). Segments ca 185 (H) (posterior amputee), ca 200 (P1). Form moderately stout, anterior end club-shaped though apically tapering, clitellar region wider; segments III-XIII strongly biannulate, clitellar and more posterior segments weakly biannulate. Pigmented reddish brown; pale ventrally. Prostomium pro-epilobous but

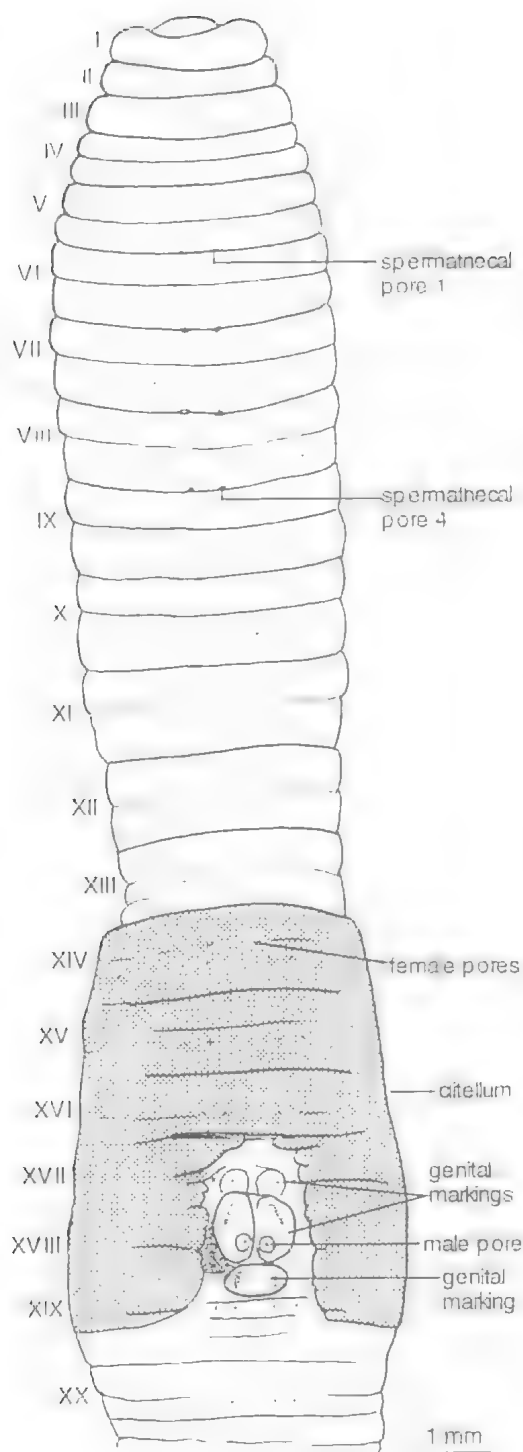


FIG. 1. *Notoscolex bukeri* sp. nov., holotype. Ventral view of fore- and mid-body.

broken up by longitudinal and transverse fissures extending the length of peristomium. First dorsal pore 4/5. Setae small, discernible with difficulty, clearest ventrally on clitellum; in 8 longitudinal rows, commencing on II, *c* and *d* caudally with pale epidermal areolae; *a* and *b* absent in XVIII; in XI (XII not clear), *aa*: *ab*: *bc*: *cd*: *dd* = 8.5: 5: 19: 6: 50%; caudally setal lines *c* and *d* and occasionally *b* irregular; *d* lines becoming irregular shortly behind clitellum. Nephropores not externally visible. Clitellum annular, well developed, thick and rigid, embracing XIV-XIX; interrupted ventrally in XVII-XIX; intersegmental furrows and dorsal pores visible though weak; setae retained. Male pores on inconspicuous small circular papillae median to *a* lines in XVIII; each papilla lying near inner posterior border of a flat, ear-shaped genital marking with slightly raised margin, the two markings conjoined across midline anteriorly and filling XVIII longitudinally. A further genital marking, also flattened with raised margin, but forming a single midventral transverse ellipse, presetally in XIX; both sets of markings extending laterally into *ab*. Female pores paired anteromedian to setae *a* of XIV. Spermathecal pores 4 pairs in 5/6-8/9, minute points median to *a* lines (Holotype).

Some anterior septa strongly thickened; 9/10-11/12 very thick. Dorsal blood vessel paired segmentally, unpaired at septa, in VII-XVI and possibly further posteriorly, the two slender halves widely divergent so as to form a diamond pattern in each segment; last hearts in XII, those in X-XII (all very slender) with their major connection to supra-oesophageal vessel which is at least partly double. Gizzard very large but flaccid in V, enclosed in septa 5/6 and 6/7; preceded by an equally wide pharyngeal mass. Oesophagus lacking calciferous glands. Intestine commencing in XVII (fragmentary). Meronephric; forebody segments with forests of minute (astomate?) parietal micromeronephridia. Caudally with transverse rows of few astomate, integumentary micromeronephridia with, on each side of nerve cord, a median stomate exonephric megameronephridium, funnel with long preseptal neck. Large iridescent sperm funnels and copious sperm masses free in X and XI; small, compact slightly lobulated seminal vesicles in IX and XII, on their posterior and anterior septa, respectively, but also a pair on posterior septum of VIII. Small ovaries in XIII. Prostates elongate, flattened racemose (tubuloracemose?), extending laterally,

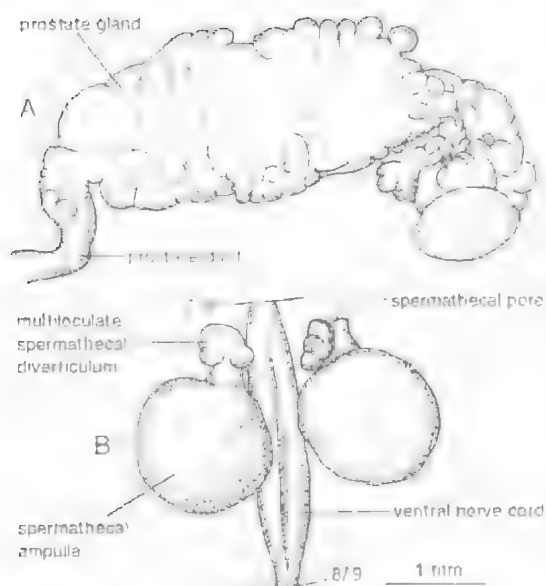


FIG. 2. *Notoscolex bakeri* sp. nov., paratype 1. A, dorsal view of right prostate. B, dorsal view of spermathecae of VIII, *in situ*.

restricted to XVIII; tongue-like with lobulated surface, each gland with single ectal bend; duct short, narrow and flaccid, lacking a muscular sheath. Penial setae absent. Spermathecae 4 pairs opening anteriorly in their segments, each with subspheroidal ampulla, a wide, somewhat shorter ectally tapering duct; and a large, sessile, multiloculate iridescent diverticulum, usually with three lobes, which joins ectal end of duct; size uniform (Paratype 1).

ETYMOLOGY. For Dr Geoffrey Baker, who provided this collection, in recognition of his contributions to earthworm ecology in Australia.

REMARKS. *N. montiskosciuskoi* Jamieson, 1973, is the only other species of *Notoscolex* with four pairs of spermathecal pores and, like *N. bakeri*, has a double dorsal vessel (double also in *N. cameroni*). It differs from *N. bakeri* in the configuration of genital markings which form ill-defined transverse slightly tumid strips one in front of, the other behind the equators of segments XVIII–XXII; those in XVIII between the male papillae. *N. bakeri* further differs in the absence of extramural calciferous glands; in lacking penial setae, in the auxiliary seminal vesicles, in VIII; and in the multiloculate, not simple clavate form of the spermathecal diverticula.

Despite the absence of calciferous glands in *N. bakeri*, similarities with *N. montiskosciuskoi* and the geographical proximity suggest that they are sister-species.

***Spenceriella* Michaelson, 1907.
emend. Jamieson, 2000**

Spenceriella Michaelson, 1907: 161.

Spenceriella (emend.): Jamieson, 2000, 1123.

DIAGNOSIS. Perichaetini; setae 16 or more per segment. A pair of combined ♂ and prostatic pores in segment XVIII. Spermathecal pores intersegmental. Gizzard in V well-developed or rudimentary. Calciferous glands 3 or 4 pairs in X–XII, XIII, or absent. Intestine acaeate. Meronephric; bucco-pharyngeal tufts present or absent; oesophageal nephridia astomate or stomate; caudal nephridia stomate (and astomate?); nephridia in regions in which they are stomate (always?) with a median preseptal funnel and multiple intrasegmental funnels. Caudal enteronephry present or, more commonly, absent. Rarely with nephridial bladders. No setae median to the male pores. Prostates racemose or tubuloracemose. Spermathecae diverticulate.

REMARKS. *Spenceriella* occurs in the Eastern Subregion, Kosciusko Division of Australia (*sensu* Kikkawa & Pearce, 1969); Lord Howe Island and Norfolk Island and the Western Subregion Darling Basin province (Jamieson, 2000). *Spenceriella* as redefined by Jamieson (2000), differs from *Anisochaeta* Beddard, 1890, in having multiple intrasegmental (not preseptal) nephrostomes, a less extensive series of calciferous glands (if present), and more numerous setae which are not in the anisochaetin arrangement. It differs from *Gemascolex* in having segmental not intersegmental genital markings and multiple intrasegmental (not preseptal) nephrostomes.

The four species of *Spenceriella* described here are referable to the *S. notabilis*-group (*Spenceriella* s. s.) of Jamieson (2000).

***Spenceriella bywongensis* sp. nov.
(Figs 3–8)**

MATERIAL. HOLOTYPE (clitellate) QM G 218235. PARATYPES 1–5 (weakly clitellate) QMG218236–218240. All from A.C.T., 35°10'S, 149°20'E, 'Bywong', Sutton, ca 20 km NE of Canberra, improved pasture, July 2000. CSIRO sample 'B'. PARATYPES 6–8 QMG218241–218243, 'Gold Creek', NE of Gungahlin, Canberra, J. Seown, July 2000. CSIRO sample 'D'; faintly clitellate.

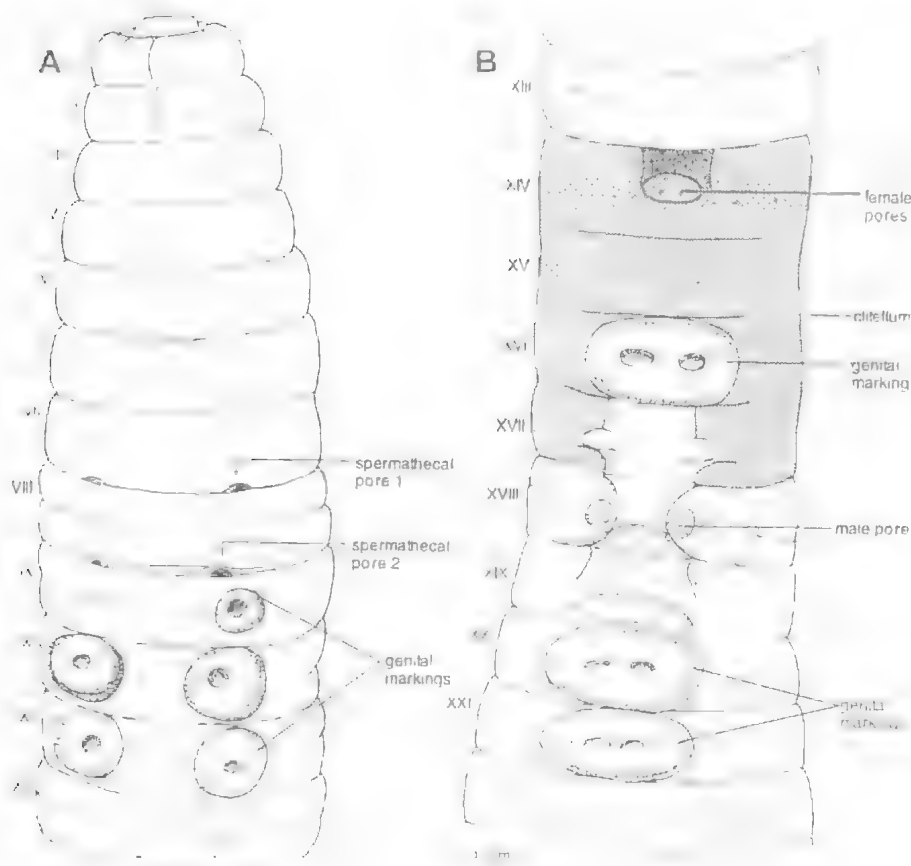


FIG. 3. *Spenceriella hywongensis* sp. nov., holotype. Ventral view. A, forebody; B, midbody.

DESCRIPTION. Length (clitellate specimens) 65-86mm, mean 75mm (II, P1-5). Width 3mm. Segments 97 (P3 is shortest)-106 (Holotype is longest). Form (as preserved) slender and elongate, cylindrical, tapering at each end, with no clubbing; slightly wider at clitellum than elsewhere. Postclitellar segments weakly triannulate. Pigmentless buff in ethanol. Prostomium epilobous 2/3 or tanylobous. Peristomium bisected ventrally. First dorsal pore 5/6. Setae per segment 20 in XII and caudally; in forebody *aa* about 4 *ab* but *ab* smaller than *bc*; \approx less than twice adjacent intervals. All rows regular. Clitellum XIV-XVII (=4 segments): annular but interrupted ventrally, in *aa*, in XVII; intersegmental furrows obscured dorsally, dorsal pores and setae clearly visible. Male pores minute but distinct, in *a* lines of XVIII, each near median aspect of a large circular porophore which fills XVIII longitudinally and extends slightly median of *a* and well laterally, beyond *c*; porophore more

sharply defined medianly than laterally, on transversely oval porophores; each male pore on small circular papilla on porophore. Genital markings: prominent circular eminences, in IX-XI; unilateral left in IX in II; right in P2, P5; absent from IX in others; paired in X and XI (constant); each with conspicuous immediately presetal pore-like centre but prominence extending both pre- and post-setally. Posterior markings: midventral oval pads filling their segments longitudinally and extending laterally of *b* lines, in XVI, XX and XXI (constant in the 3 segments), or XXII also (P1, P2, 'pore' unilateral left; P5, 'pore' paired) each with 2 transversely elongated 'pores' immediately anterior to and including setal arc, excepting P1 in which in XVI and XXII pore-like marking is unpaired midventral and is hardly bifid in XX and XXI; a slightly posterior crescentic swelling in XIX (H) and a midventral pad in XVII (P3, P5); in only P2 a pair of widely separated porelike markings in

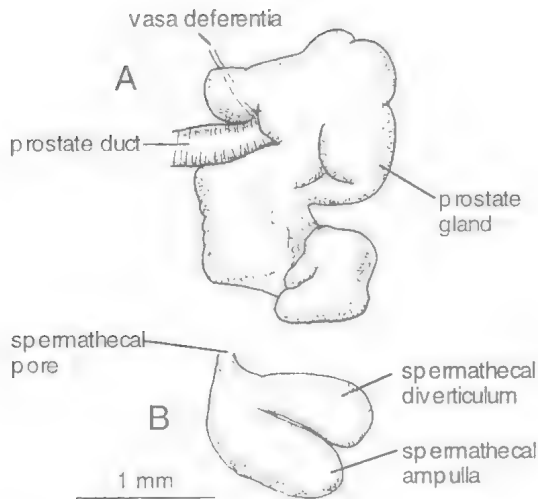


FIG. 4. *Spenceriella bywongensis* sp. nov., Bywong material, holotype. A, dorsal view of right prostate; B, dorsal view of right spermatheca of VIII.

XIX. Female pores paired on XIV, just anterior to setal arc, about one-third *aa* apart, in common glandular field. Spermathecal pores 2 pairs of large eye-like papillae, in 7/8 and 8/9, centred approximately in *b* lines.

Several anterior septa moderately thickened; 8/9 strongest. Dorsal blood vessel continuous onto pharynx; hearts in X-XII latero-oesophageal with chief origin from calciferous vessel, near origin of latter from supra-oesophageal vessel; commissurals of IX anterior dorsoventral only. Gizzard large, barrel-shaped in V, with muscular sheen but readily depressed; extending to level of intersegment 8/9 posteriorly, septa 5/6 and 6/7 funnel-shaped around it. Oesophagus with 3 pairs of very large almost spherical calciferous glands, in X, XI and XII, each with its ventromedian aspect narrowly attached to oesophagus. Intestinal origin XVI, superficially appearing to commence in XV but septum 15/16 adherent to its anterior limit; acaecate; a well-developed dorsal typhlosole commencing though there rudimentary in XVIII. Meronephric with pairs of small tufted nephridia ventrally in III, IV and V; first 2 pairs small, those in V very large; all apparently exonephric; reducing to parietal but not numerous micromeronephridia by clitellar region. A large median preseptal funnel and post-septal (intrasegmental) funnels demonstrated for caudal nephridia, confirming placement in *Spenceriella*; all exonephric. Ovaries in XIII, an exceptionally large palmate

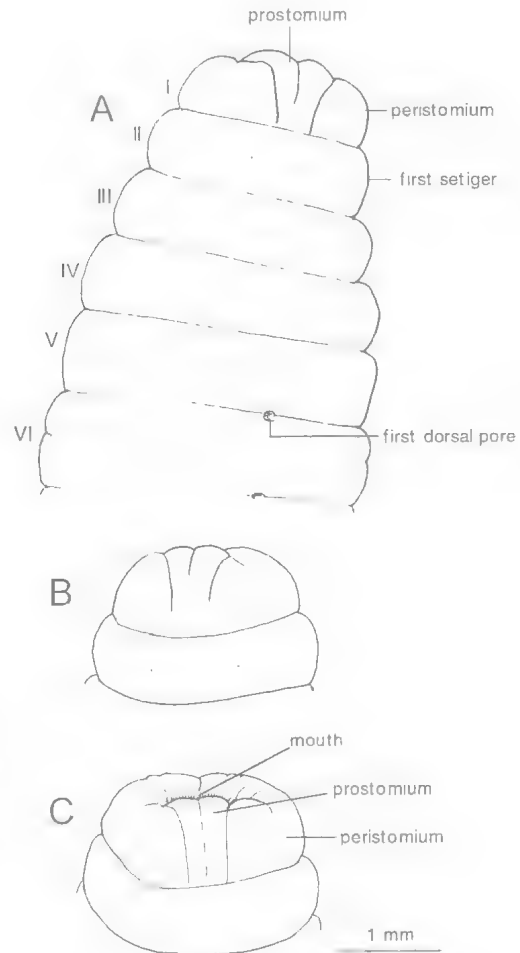


FIG. 5. *Spenceriella bywongensis* sp. nov. Bywong material. Dorsal view of prostomial region. A, holotype; B, paratype 1; C, paratype 3.

pair with numerous strings of large oocytes, and paired thick funnels; conspicuous ovisacs on anterior wall of XIV, only slightly smaller than ovaries and with several oocytes projecting. Holandric, a pair of large testes and funnels in each of X and XI (only those in X notably iridescent), embedded in large free sperm masses; large racemose seminal vesicles in IX and XII, posterior pair larger. Prostates a pair of large, racemose glands, in XVIII-XX, but resolvable into a flattened S-shape the anterior half of which is enlarged and forms a square outline; vasa deferentia joining ental end of duct [as in *S. macleayi*]; duct thick and with muscular sheen, shorter than width of square portion of gland, extending directly median. Penial setae absent. Spermathecae 2 pairs, in VIII and IX with

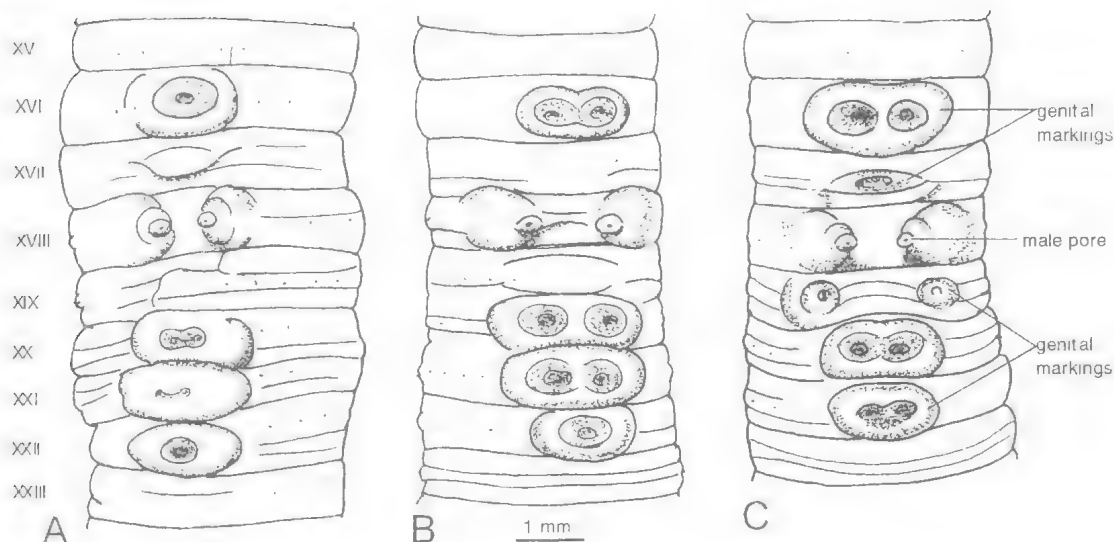


FIG. 6. *Spenceriella bywongensis* sp. nov. Bywong material. Variation in configuration of posterior genital markings. A, paratype 1; B, paratype 2; C, paratype 3.

large ovoid or polex-shaped ampullae tapering to ducts each bearing near its ectal end a thickly digitiform diverticulum which is a little shorter than, and (on right VIII) may be almost as wide, as ampulla; common duct of ampulla and diverticulum scarcely developed.

The 3 Gold Creek specimens (P6-8) are closely similar to those from Bywong but differ in having paired pore-like markings in XVII (P6, P8) and large markings of this type in XIX (constant); furthermore, one specimen has a marking (unpaired, midventral) on XXII. In detail, there are paired (sometimes unilateral) pore-like markings in IX (P6 only, unilateral left); X and XI (constant but unilateral left in P7); XVI (constant); XVII (P6, P8, absent P7); XIX-XXI (constant); and midventral marking in XXII in P7. Paired markings in XIX-XXI are progressively closer, posteriad, to the midventral line, those in XXI being on common pad.

ETYMOLOGY. From the type locality, Bywong.

REMARKS. Other species of *Spenceriella* with 2 pairs of spermathecal pores and 3 pairs of calciferous glands, in X-XII, are *S. australis* (Fletcher, 1886) from Burrawang and Mt Wilson, NSW, *S. indissimilis* (Fletcher, 1889), from Lake Alexandrina, S. Australia, and *S. montanus* (Spencer, 1900), from Mt Baw Baw, Victoria. *S. australis* differs from *S. bywongensis* in the wide separation of the spermathecal pores and a very different configuration of the genital markings.

The little known *S. montanus* appears to differ in having unpaired, not paired genital markings in X and XI, together with those in XIX and XX. The geographically distant *S. indissimilis* is the most similar to *S. bywongensis* but differs, among other respects, in restriction of its anterior genital markings (in some or all of VII-X) to the presetal parts of their segments; in absence of any indication of pairing in the posterior genital markings; the closer pairing of the spermathecal and male pores; the smaller gizzard; and the bipartite condition of each prostate. The wide geographic separation of *S. bywongensis*, *S. montanus*, and *S. indissimilis* further supports specific distinction.

***Spenceriella hamiltoni* (Fletcher, 1887) (Figs 9, 10)**

Perichaeta hamiltoni Fletcher, 1887: 399-400

Megascolex hamiltoni; Beddard, 1895: 373.

Anisochaeta hamiltoni; Blakemore, 2000: 4.

Spenceriella hamiltoni; Jamieson, 2000: 1225-1227, Fig. 41.28.

Anisochaeta chani Blakemore, 2000: 18-19. New Synonymy.

Spenceriella chani; Jamieson, 2000: 1193-1195.

NEW RECORD. N.S.W., ca 5km S of Neville (33°43'S.149°13'E.), near Blayney and Bathurst, from improved pasture (CSIRO sample 'E - dark head'); 2 weakly clitellate, QMG218244-218245, and 2 (unregistered) acitellate, macerated specimens.

DESCRIPTION. Length 134-150mm (specimens 1 and 2 respectively). Width ca 6.4mm. Segments 128-145mm. Form (as preserved)

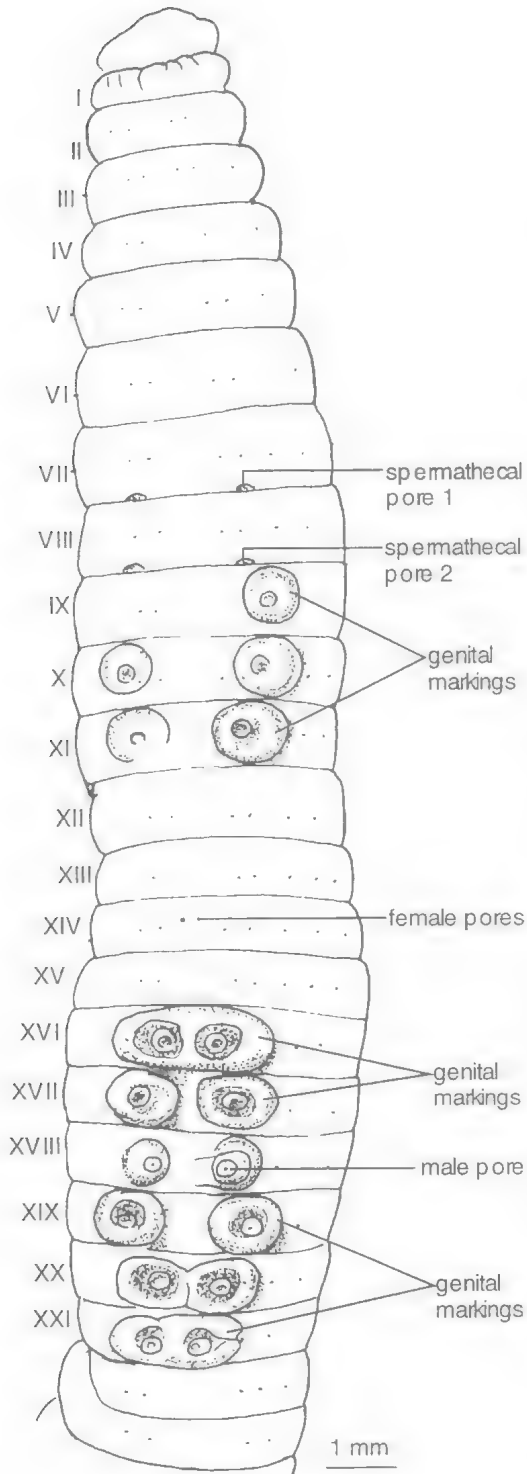


FIG. 7. *Spenceriella bywongensis* sp. nov. Gold Creek material. Paratype 6. Ventral view of fore- and mid-body.

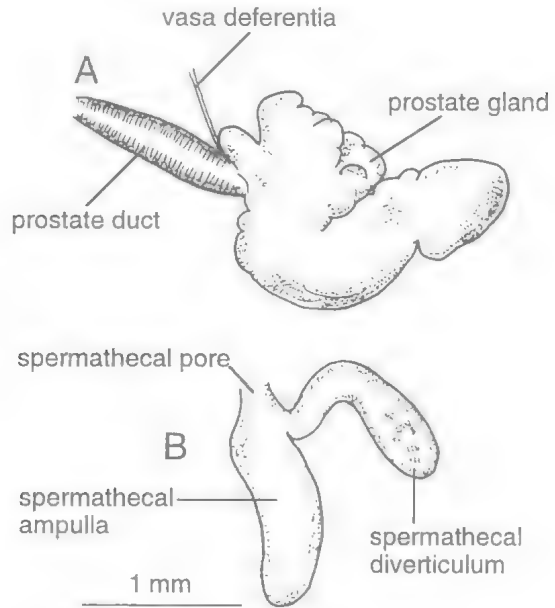


FIG. 8. *Spenceriella bywongensis* sp. nov. Gold Creek material. Paratype 6. A, dorsal view of right prostate; B, dorsal view of right spermatheca of VIII.

slender, elongate, cylindrical, tapering at each end, slightly club-shaped anteriorly; clitellum about as wide as club-shaped region. Segments simple, lacking secondary annulation. Darkly pigmented, pale ventrally, in ethanol. Prostomium narrow epilobous 2/3, open. Peristomium weakly bisected ventrally. First dorsal pore 5/6. Setae per segment: 18 in XII, 20 in XX; about 28 caudally; in forebody *aa* ca 3.5 *ab* but *ab* smaller than *cd* ($cd:ab = 1.5$); dorsal break large, *zz* = about 4 *zy*. All rows regular, with occasional slight divergence. Clitellum weakly developed, from redder coloration, XIV–XVII (= 4 segments); annular?, intersegmental furrows and setae clearly visible; dorsal pores obscured (but minute elsewhere). Male pores in XVIII, each projecting medially from a large mound; minute but distinct, very slightly median of *a* lines of XVIII, each on small but distinct circular porophore which fills about two-thirds of length of XVIII, is continuous laterally with longitudinal prominence which occupies whole length of segment and extends laterally, beyond *c*; prominence more sharply defined medially than laterally. Genital markings: pre- and post-setal paired pore-like markings faintly indicated on common transverse pad, on X. Paired pore-like markings close to midventrum immediately postsetal in XVI and XVII and

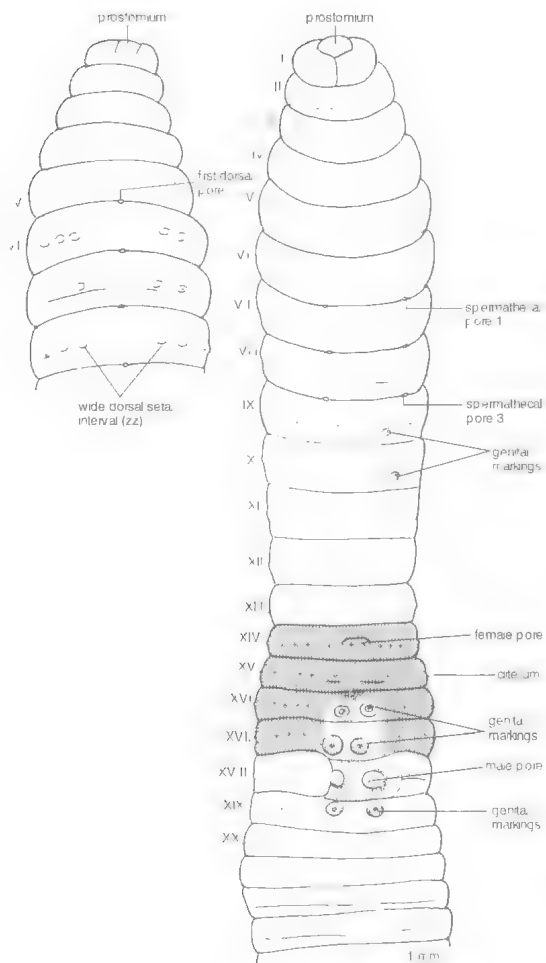


FIG. 9. *Spenceriella hamiltoni* (Fletcher, 1887). A, dorsal view of prostomial region; B, ventral view of fore- and mid-body of specimen 2.

presetally and slightly more laterally, though anteromedial to setae *a* in XIX. Female pores paired on XIV, just anterior to setal arc, close together in a common glandular field. Spermathecal pores 3 pairs of small but sharply defined open slits, in 6/7, 7/8 and 8/9, in setal lines *b*.

Several anterior septa thickened; 8/9-11/12 strongly. Dorsal blood vessel single, continuous onto pharynx; hearts in X-XII latero-oesophageal with chief origin from calciferous vessel, near origin of latter from supra-oesophageal vessel; commissurals of IX anterior originating from dorsal vessel only. Gizzard large, barrel-shaped in V, firmly muscular; extending to level of

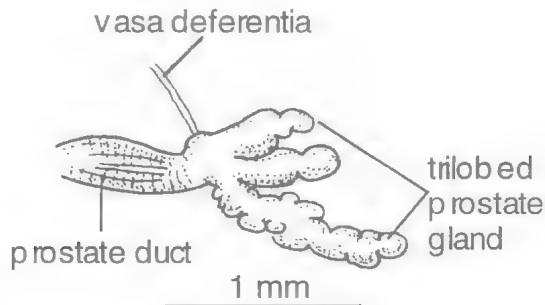


FIG. 10. *Spenceriella hamiltoni* (Fletcher, 1887). Dorsal view of (immature) right prostate of specimen 2.

intersegment 8/9 posteriorly, septa 5/6 and 6/7 funnel-shaped around it. Oesophagus with 3 pairs of large almost spherical calciferous glands, in X, XI and XII, each broadly attached to oesophagus but separated by a deep trench middorsally. Intestinal origin XVI; acaecate; a low ridge but no true dorsal typhlosome present. Intestinal contents unusual in containing very little fine grit, but with sparse (siliceous?) grains and filled with dense masses of what appear to be strips of grass blades. Meronephric, nephridia commencing in II; forming large masses in III-VI but not united as tufts; all apparently exonephric; reducing to parietal but not numerous micromeronephridia by XII or XIII. A single median preseptal funnel (not multiple funnels) demonstrated on each side of nerve cord for caudal nephridia, confirming placement in *Spenceriella*; all exonephric. Sparse ovaries with visible oocytes and small funnels, in XIII; ovisacs not found. Holandric, seminal funnels in each of X and XI, lacking spermatozoal iridescence; racemose seminal vesicles in IX and XII, posterior pair tortuous, vermiform (incompletely mature). Prostates a pair of racemose glands, in XVIII, incompletely mature; divided from ental end of duct into three major, elongate lobes; vasa deferentia joining anterior lobe near its base; duct wide and fusiform. Penial setae absent. Spermathecae 3 pairs, small and immature, in VII, VIII and IX with ovoid ampullae tapering to ducts each bearing near its ectal end a small polex-shaped diverticulum; common duct of ampulla and diverticulum scarcely developed.

REMARKS. The clearly phytophagous nature of this species, demonstrated in the new material, correlates with the dark pigmentation of the body

as it presumably emerges above ground to remove portions of grass blades.

This material conforms very closely to the description of *Spenceriella* (= *Anisochaeta*) *chani* (Blakemore, 2000), reported from Neville and Cowra, even to the multilobed prostates. However, there seems no valid reason to separate it, or *chani*, from the prior *S. hamiltoni* (Fletcher, 1887) which was collected from Cowra and Oberon by Easton, as reported in Jamieson (2000). These localities are respectively 51 km W and 59 km E of Neville. The type locality of *S. hamiltoni*, Guntawang, is about 150 km N of Neville. The ♂ pore on the right side in the putative syntype of *S. hamiltoni* (Jamieson, 2000) is near *a* line, the disposition of genital markings, albeit absent in XVI, resembles that in *S. chani* and the prostates are again multilobed. Location of each of the small ♂ porophores, in the new material, median to a longitudinal prominence is not here considered a significant difference from *hamiltoni* and *chani* as in both of these there is a tendency to lateral enlargement of the prostate porophores. The possibility that *S. hamiltoni* is a junior synonym of *S. australis* (Fletcher, 1886) remains to be investigated.

***Spenceriella macleayi* (Fletcher, 1889)**
(Figs 11)

Perichaeta macleayi Fletcher, 1889: 1556-1558.

Perichaeta macleayi var. a, b and c; Fletcher, 1890: 1004-1007.

Megascolex macleayi (Fletcher); Beddard, 1895: 376.

Spenceriella macleayi (Fletcher); Blakemore & Elton, 1994: 251-254, fig. 1; Jamieson, 2000: 1254-1258, fig. 41.43-41.47.

Anisochaeta macleayi (Fletcher); Blakemore, 2000: 4.

? *Anisochaeta filix* Blakemore, 2000: 21-22, Fig. 11.

NEW RECORDS: A.C.T., 35°10'S, 149°20'E, 'Bywong', Sutton, ca 20 km NE of Canberra, in improved pasture, July 2000. 8 clitellate specimens. CSIRO sample 'A, Dark head'. QMG218246-218253. 'Gold Creek', native pasture just NE of Gungahlin, Canberra, J. Scown, 2 July 2000. CSIRO sample 'C. Native 1'; 3 clitellate; 3 (unregistered) a clitellate specimens. QMG218254-218256.

DESCRIPTION. Length of clitellate specimens from both localities 55-95 (mean 70) mm. Width (midclitellar) 3.8 mm; segments 87 (A, illustrated specimen). Colour in ethanol dark purplish grey-brown dorsally and laterally, especially anterior to clitellum, setal areolae and ventrum pale. Prostomium epilobous 3/4, closed, wedge-shaped. Peristomium bisected ventrally. First dorsal pore 5/6. Setae per segment 22 in XII. Clitellum annular, XIII-XVII. Genital markings (constant in 8 A and 3 C clitellate specimens): a

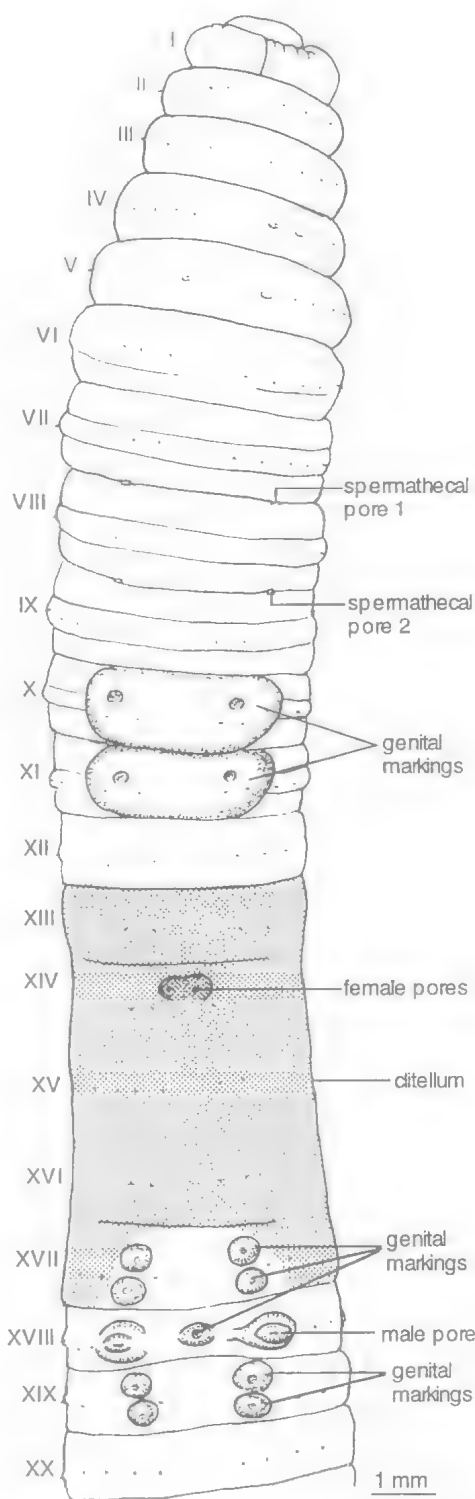


FIG. 11. *Spenceriella macleayi* (Fletcher, 1889). Ventral view of fore- and mid-body

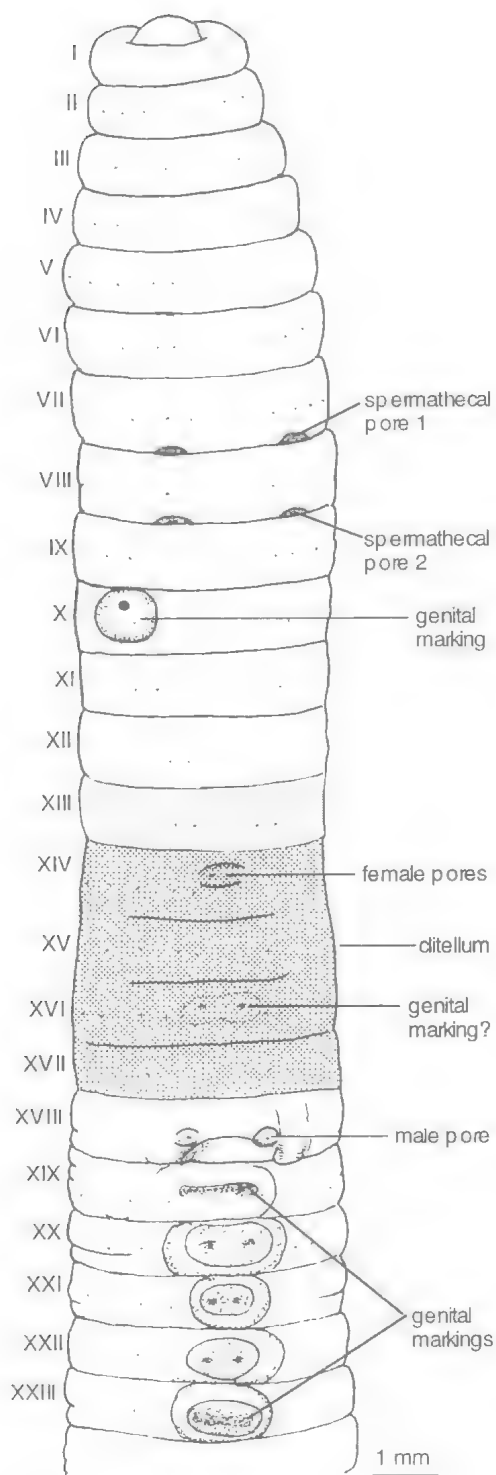


FIG. 12. *Spenceriella nevillei* sp. nov. Holotype. Ventral view of fore- and mid-body of holotype.

transverse pad on each of X and XI, extending laterally to about *c* lines and filling segment longitudinally, each with pair of pore like presetal circular markings in *ab*; a pair of presetal and postsetal circular papillae with pore-like centre in each of segments XVII and XIX, most anterior and posterior pair of four, slightly more median than other two and all slightly median of line of male pores; an additional, midventral, eye-like marking equatorial in XVIII between male porophores. Male pores in *bc* lines on small elliptical papillae which are situated on larger porophores which do not, however, reach anterior and posterior borders of XVIII. Female pores paired on XIV, presetally and about $\frac{1}{3}$ *aa* apart, in a common glandular field. Spermathecal pores 2 minute pairs, in $\frac{7}{8}$ and $\frac{8}{9}$, in or slightly ventral of *c* lines.

Dorsal blood vessel single, continuous onto pharynx. Last hearts in XII. Gizzard large, a posteriorly slightly tapering cylinder in V, moderately muscular. Prostates large, racemose bipartite glands (C) or tortuous racemose, in XVIII to as far as XXI (A). Spermathecae 2 pairs, in VIII and IX with large subspherical or elongate ampullae tapering to ducts each bearing near ectal end a large, clavate diverticulum (A, C).

REMARKS. The combination of calciferous glands limited to XI and XII with the particular arrangement of genital markings is diagnostic of *S. macleayi*. Fletcher (1889) noted as a variant a midventral marking in XVIII, also seen here. Specimens from Manning River, NSW, identified as *S. raymondiana* Fletcher (1887) by Easton (unpubl.) with similar restriction of calciferous glands to XI and XII are referred below to a new species which differs, among other respects, from *S. macleayi* in having 3 pairs of spermathecae. They were tentatively described as *S. raymondiana* by Jamieson (2000). The only other species of *Spenceriella* with 2 pairs of calciferous glands is *S. filix* (Blakemore, 2000), collected by Easton from Tree Fern Valley, NSW. It appears probable, from its description, that it is conspecific with *S. macleayi*.

S. macleayi is widespread in NSW, being known from Elizabeth Bay, Sydney (the type locality); Mt Wilson; Mt Lawson; Burrawang; Mt Victoria; Raymond Terrace; Morpeth; Richmond; Queenscliff; Mt Tomah; Bunadoon, Moss Vale District; Upper Manning River; and Old Newington (details in Jamieson, 2000).

***Spenceriella nevillei* sp. nov.**
(Figs 12, 13)

MATERIAL EXAMINED. HOLOTYPE QMG218257. PARATYPES 1 & 2, QMG218258–218259. All from ca 5 km S of Neville (33°43'S, 149°13'E), near Blayney and Bathurst, NSW, from improved pasture (CSIRO sample 'F'). Two weakly clitellate; one (excluded from type series) acitellate.

DESCRIPTION. Length (clitellate specimens) 80–115 mm (H, P₁). Width (forebody) 4 mm. Segments 91–129. Form (as preserved) slender and elongate, cylindrical, tapering at each end, slightly club-shaped in forebody; clitellum forming a narrower cylinder. Segments weakly triannulate. Pigmentless buff in ethanol. Prostomium tanylobous, its lateral borders gradually converging posteriad but posteriorly so weakly defined that it appears epilobous. Peristomium bisected ventrally. First dorsal pore 5/6. Setae often difficult to discern, about 18–20 in XII and caudally; in forebody *aa* about 2.6 *ab* but *ab* smaller than *bc*; *zz* in forebody less than twice adjacent intervals, not an appreciable break in setal circlet behind clitellum; setal rows mostly regular. Clitellum XIII–XVII (=5 segments); less developed in XIII; annular but interrupted ventrally, to approximately *c* lines, in XVI and XVII; intersegmental furrows and dorsal pores, except 13/14, obscured dorsally, setae clearly visible. Male pores minute but distinct, in *a* lines of XVIII, each on a very small transversely elliptical papilla which is bordered laterally by a longitudinal prominence which extends length of segment. Genital markings a weakly visible circular disc on right side only (H) or paired (P₁) almost filling segment longitudinally and bearing a pore-like presetal marking in ca *c* line. Posterior genital markings consisting of faintly visible midventral pads with raised rims in each of XX–XXIII, first 3 of them with suggestions of paired pore-like markings. A suggestion of ventral glandularity in XVI is probably not a true genital marking; a marking in XIX is also doubtful (H). Posterior genital markings in the paratypes are too poorly defined for certain determination of their distribution. Female pores paired on XIV, just anterior to setal arc, about one third *aa* apart, in a common glandular field. Spermathecal pores 2 pairs of large eye-like papillae, in 7/8 and 8/9, centred approximately in *b* lines.

Several anterior septa moderately thickened; 8/9–10/11 strongest. Dorsal blood vessel continuous onto pharynx; dorsoventral commissurals in X–XII forming large hearts. Gizzard

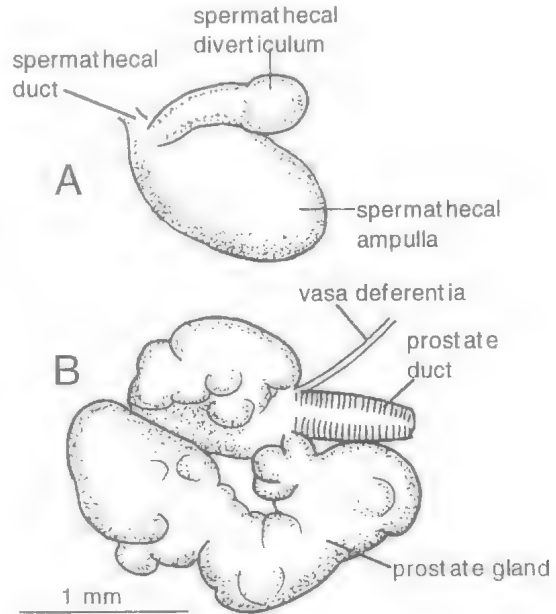


FIG. 13. *Spenceriella nevillei* sp. nov. Holotype. A, dorsal view of right spermatheca of IX; B, dorsal view of left prostate.

in V, large, wider anteriorly than posteriorly, with muscular sheen but readily depressed; extending to level of intersegment 8/9 posteriorly, septa 5/6 and 6/7 funnel-shaped around it. Oesophagus with 4 pairs of large reniform calciferous glands, in X–XIII (holotype and paratype), a short duct from hilus connecting to dorsolateral aspect of oesophagus; each pair of glands supplied by bifurcation of supra-oesophageal vessel present anteriorly in segment but does not continue posteriorly of pair of glands and originates anteriorly from dorsal vessel. Intestinal origin XVI; acaecate; a well-developed dorsal typhlosole commencing in XVIII–XIX though there rudimentary. Meronephric with at least 3 pairs of tufted nephridia in buccopharyngeal region with thick anteriorly running (enteronephric?) ducts; parietal micromeronephridia, about as numerous as setae in clitellar region. Ovaries not visible (H) or small, bushy (P₁). Holandric, a pair of free sperm masses and funnels (with negligible spermatozoal iridescence) seen in each of X and XI; large laterally extensive racemose seminal vesicles in IX and XII, posterior pair larger. Prostates S-shaped tubuloracemose; a stout muscular duct of moderate length arising from anterior limit where it is joined basally by combined vasa deferentia. Penial setae absent.

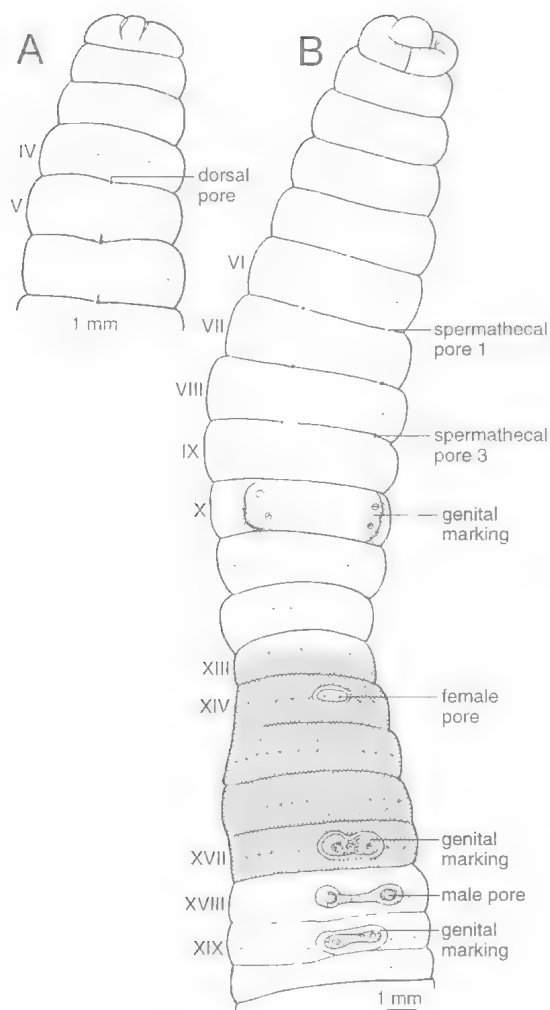


FIG. 14. *Spenceriella manningi* sp. nov. Holotype. A, prostomium; B, ventral view of fore- and mid-body.

Spermathecae 2 pairs, in VIII and IX with large ovoid ampullae tapering to ducts each bearing near its ectal end a clavate diverticulum which is a little shorter than ampulla; common duct of ampulla and diverticulum scarcely developed.

ETYMOLOGY. From near Neville.

REMARKS. Two pairs of spermathecae and 4 pairs of calciferous glands, as in *S. nevillei*, are also seen in *S. monticola* (Fletcher, 1887) and *S. calpetana* (Blakemore, 2000). *S. monticola* differs from *S. nevillei* in being larger, pigmented reddish brown, with more setae (16-50); and a different configuration of genital markings.

S. calpetana differs, among other respects, in having about 60 setae per segment, a markedly different configuration of genital markings, seminal vesicles in XI and XII; and no typhlosole.

***Spenceriella manningi* sp. nov.**
(Fig. 14,15)

Spenceriella raymondiana (part.) Jamieson, 2000: 1293-1297, fig. 41.70, 41.71.

MATERIAL. HOLOTYPE AM W197644 from 31°49'S, 151°56'E., Upper Manning River, NSW, coll. and ident. as *S. raymondiana* by E. Easton, 1983.

DESCRIPTION. Length 165mm. Width (mid-clitellar) 71mm. Segments 117. Prostomium epilobous, almost tanylobous, with wide, deep lateral grooves, slightly convergent posteriad. Prostomium bisected ventrally. First dorsal pore 4/5. Setae per segment: in XII 26; caudally 32. In XII *aa*: *ab*: *zz* = 14: 4.5: 6.0; dorsal and ventral breaks clearly visible preclitellar; not apparent behind clitellum but *aa* becoming wide caudally; no evident irregularity. Clitellum annular, limits indistinct but dorsally from setal zone of XIII to posterior XVII; dorsal pores of 14/15-16/17 occluded. Male pores in *a* lines on small rounded papillae surrounded by dark glandular border with narrow connection across ventral midline with that of other side. Genital markings a pair of small pore-like markings presetal in *bc* and post-setally in *b* lines of X; 2 'pores' of a side lying on a common raised glandular pad which is well defined laterally but not medianly. A pair of pore-like markings immediately presetal and median to *a* lines of XVII, each surrounded by a dark glandular border which is broadly confluent with that of other side. Similar markings in XIX with a narrower connecting zone. Female pores shortly presetal, well median of *a* lines, in a common dark oval field with a narrow, tumid, pale margin. Spermathecal pores 3 pairs of minute orifices apparent only on opening up inter-segmental grooves, in 6/7, 7/8 and 8/9, shortly below *b* lines.

Septa 7/8-13/14, strong. Dorsal blood vessel single, continuous onto pharynx; last hearts in XII; those in XI and XII, only, latero-oesophageal. Supra-oesophageal recognizable in XI and XII. Gizzard in V, broad, cylindrical and strongly muscular, preceded by a short, almost equally broad proventriculus. Oesophagus with a pair of large, extramural calciferous glands, each with a narrow posterior connection to gut, in each of segments XI and XII; glands with numerous

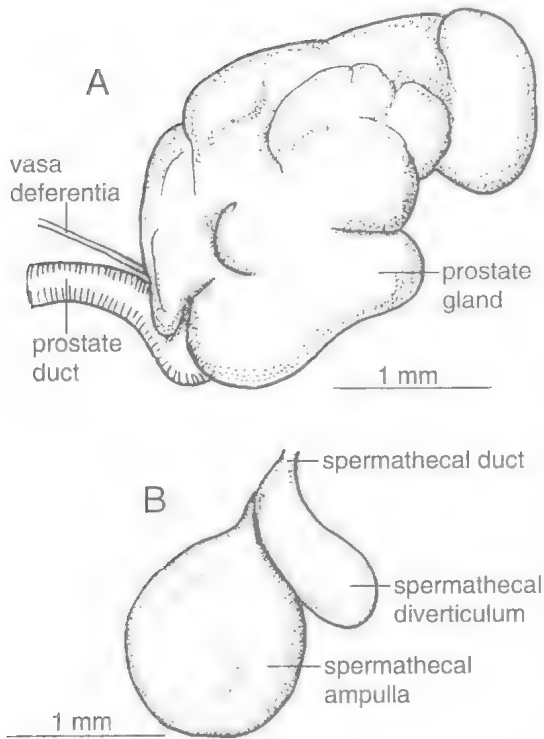


FIG. 15. *Spenceriella manningi* sp. nov. Holotype. A, right prostate; B, right spermatheca of IX.

narrow internal longitudinal septa. Intestine commencing XVI but pushing septum 15/16 close to 14/15; no definite typhlosome seen. Nephridia tufted in III and IV and, less compact, in V. Transverse bands of apparently astomate meronephridia posterior in succeeding segments of forebody. Caudally with dense bands of meronephridia filling segments; no presepatal funnels seen; some intrasegmental funnels tentatively identified. Large sperm masses in X and XI invest iridescent sperm funnels which lie posteriorly in each segment; the masses possibly enclosed in thin, membranous testis-sacs. Seminal vesicles large, racemose, in IX and XII. Ovaries webs of numerous large oocytes in XIII. Large morula-like ovisacs on anterior walls of XIV. Prostates appearing to be compactly tubuloracemose but not resolvable into distinct tubes, therefore racemose; restricted to XVIII, each with a short, muscular duct which is joined, near its junction with gland, by a thick vas deferens. Spermathecae 3 pairs, each with somewhat flattened subspheroidal ampulla, narrowing with no distinct duct to body wall and joined ectally by clavate uniloculate

diverticulum of about equal length (1.4mm), with spermatozoal iridescence.

ETYMOLOGY. From the type locality.

REMARKS. Jamieson (2000) stated that in the absence of type material, it was uncertain that the material identified by Easton as *S. raymondiana*, including that from the Upper Manning River (W197644 ex 1515), was referable to this species, in which it was provisionally placed. The Manning River material is here distinguished as *S. manningi*. The remaining Easton material is not available for examination.

Only *S. macleayi* Fletcher, 1889, and the probable junior synonym of the latter, *A. filix* Blakemore, 2000, resemble *S. manningi* in having calciferous glands restricted to 2 pairs, in all 3 taxa being in segments XI and XII. *S. manningi* differs in having 3 pairs of spermathecal pores, the other 2 taxa having 2 pairs. The genital field of *S. manningi* differs in important respects from that of *S. macleayi*.

The posterior genital field in the Manning River material is also similar to that of *S. jenolanensis*, and may indicate close relationship though that species differs in its 4 pairs of spermathecae and 4 pairs of calciferous glands, in X-XIII.

Molecular studies are required to aid elucidation of the phylogenetic relationships of these and other *Spenceriellas*.

ACKNOWLEDGEMENTS

The author is grateful to Dr. Geoffrey Baker, CSIRO, Entomology, Canberra, for providing the CSIRO material described in this paper. Dr. Pat Hutchings and Dr. Penny Barents are thanked for providing facilities in the Australian Museum. All illustrations (by camera lucida) are by the author.

LITERATURE CITED

- BEDDARD, F.E. 1890. Observations upon an American species of Perichaeta, and upon some other members of the genus. *Proceedings of the Zoological Society of London* 1890: 52-69.
- BEDDARD, F.E. 1895. *A Monograph of the Order of Oligochaeta*. Clarendon Press, Oxford.
- BLAKEMORE, R.J. 2000. New species of the earthworm genus *Anisochaeta* (Oligochaeta: Megasclecidae) from New South Wales. *Records of the Australian Museum* 52: 1-40.
- BLAKEMORE, R.J. & ELTON, K.L. 1994. A hundred-year-old worm? *Australian Zoologist* 29: 251-254.

- FLETCHER, J.J. 1886a. Notes on Australian Earthworms-Part I. Proceedings of the Linnean Society of New South Wales 1(2): 523-574.
- 1886b. Notes on Australian Earthworms-Part II. Proceedings of the Linnean Society of New South Wales 1(2): 943-973.
1887. Notes on Australian earthworms-Part III. Proceedings of the Linnean Society of New South Wales 2(2): 375-402.
1889. Notes on Australian earthworms-Part V. Proceedings of the Linnean Society of New South Wales 3(2): 1521-1558.
1890. notes on Australian earthworms-Part VI. Proceedings of the Linnean Society of New South Wales 4(2): 987-1019.
- JAMIESON, B.G.M. 1973. Earthworms (Megascolecidae: Oligochaeta) from Mount Kosciusko, Australia. Records of the Australian Museum 28: 215-252.
2000. Native Earthworms of Australia (Megascolecidae, Megascolecinae). (Science Publishers Inc.: Enfield, New Hampshire). (CD ROM).
- KIKKAWA, J. & PEARSE, K. 1969. Geographical distribution of land birds in Australia – a numerical analysis. Australian Journal of Zoology 17: 821-840.
- MICHAELSEN, W. 1907. Oligochaeta. Pp117-232. In W. Michaelsen & R. Hartmeyer (eds) Die Fauna Südwest-Australiens (Gustav Fischer: Jena).
- SPENCER, W. B. 1900. Further descriptions of Australian earthworms, Part I. Proceedings of the Royal Society of Victoria new series 13: 29-67.

STATUS OF ESTUARINE CROCODILES IN THE POPULATED COAST OF NORTHEAST QUEENSLAND

CHRISTOPHER P. KOFRON AND RUSTY SMITH

Kofron, C.P. & Smith, R. 2001 06 30: Status of Estuarine Crocodiles in the populated coast of northeast Queensland. *Memoirs of the Queensland Museum* **46**(2): 603-610. Brisbane. ISSN 0079-8835.

Tully to Cooktown encompasses 325km of coastline in northeast Queensland. During the past 50 years this area has undergone tremendous urban, rural residential and agricultural development. North of Cooktown human population density is low. Since 1990, Estuarine Crocodiles (*Crocodylus porosus*) have attacked six people in Queensland resulting in one death and five serious injuries. Two attacks occurred in the study area in Cairns during 1997 and 1998. Consequently public perception is that numbers of crocodiles have increased greatly since cessation of commercial hunting in 1974 and elimination of removal zones around cities and towns in 1991, and public concern for human safety from crocodile attack is high. We surveyed the major waterways between Tully and Cooktown for Estuarine Crocodiles from June 1996 to May 1998: Hull R, Maria Ck, Moorsby R, Johnstone R, Russell/Mulgrave R, Trinity Inlet, Barron R, Daintree R, Annan R and Endeavour R. These waterways comprise most of the habitat occupied by Estuarine Crocodiles between Tully and Cooktown. We surveyed 346km of waterway, sighting 146 crocodiles at densities 0.11/km to 1.00/km. Overall density was 0.34/km, which relative to most waterways in Cape York Peninsula is low. Contrary to public perception, the crocodile population between Tully and Cooktown is of low density. Certain human activities such as urban, rural residential and agricultural development, clearing of riparian vegetation, disturbance by motor boats, commercial gill netting in estuaries, and removal of crocodiles appear to be keeping crocodile numbers low in this area. □ *Crocodiles, north Queensland, estuarine.*

Christopher P. Kofron Queensland Parks and Wildlife Service, Northern Regional Centre, PO Box 2066, Cairns 4870, (e-mail: Chris.Kofron@env.qld.gov.au); Rusty Smith Queensland Parks and Wildlife Service, Innisfail District Office, PO Box 44, Innisfail 4860, (e-mail: Rusty.Smith@env.qld.gov.au), Australia; 24 May 2001.

The Estuarine Crocodile, *Crocodylus porosus*, is the world's largest living crocodile, with total lengths up to 9m (Groombridge, 1987). Its large size and predatory habits cause special management problems because most people do not want to live or recreate near large, dangerous, predatory wildlife. The geographic range is greater than for any other crocodile, extending from Vanuatu and Solomon Islands in the east, across northern Australia, New Guinea, Indonesia, Borneo, Philippine Islands and Southeast Asia to eastern India and Sri Lanka. Despite this enormous geographic range, its populations in most countries are very severely depleted with continuing decline (Groombridge, 1987). Prospects for survival appear to be poor except in Indonesia, Papua New Guinea and Australia (Ross, 1998).

The geographic range in Queensland extends from Fitzroy R system (23°27'S), along the eastern coast to islands of Torres Strait, along the western coast of Cape York Peninsula, to the Northern Territory. In Queensland, Estuarine

Crocodiles inhabit coastal waterways, and freshwater sections of rivers where they may travel several hundred kilometres inland (Taplin, 1987). Estuarine crocodiles are listed as 'vulnerable', if threatening processes continue (Department of Environment and Heritage, 1994).

Since 1990 Estuarine Crocodiles have attacked 6 people in Queensland resulting in 1 death and 5 serious injuries. Two recent attacks occurred in Cairns. On 28 November 1997, a man swimming at Yorkey's Knob Beach was attacked by a 2.6m crocodile, suffering puncture wounds on head, shoulder and back. On 6 February 1998, a teenage girl swimming in a mangrove-lined drain of Chinaman's Ck was attacked by a 3.1m crocodile, suffering deep puncture wounds in both legs and a broken ankle. Public perception is that crocodile numbers have increased since cessation, in 1974, of commercial hunting, and elimination, in 1991, of removal zones around cities and towns. Consequently public concern for human safety from crocodile attack is

especially high. The purpose of this study, therefore, was to determine the current status of Estuarine Crocodiles in the populated coast of northeast Queensland.

Some rivers between Tully and Cooktown were surveyed previously by Queensland National Parks and Wildlife Service from 1984-1986 (Taplin, 1989) and in 1991 (Kreiger & Fell, 1991). Although no data exist on crocodile numbers prior to commercial hunting in Queensland, crocodile numbers were apparently reduced to low levels relative to pre-hunting abundance (Taplin, 1987). It seems probable that the combination of commercial hunting and removal zones in late 1980s to early 1990s reduced crocodile numbers to very low levels within the study area. However, some people argue that these tidal waterways, mostly short and with headwaters in mountains to the west, were never a major crocodile breeding area and never contained high numbers, cooler water temperatures being a determining factor.

STUDY AREA

Cairns (16°55'S) is 119km N of Tully (17°56'S) and 169km S of Cooktown (15°28'S) on the eastern coastal plain in the Tropical Rainforest Bioregion. Rivers on the NE coast between Tully and Cooktown are not extensive. Tully to Cooktown encompasses 325km of coast, and here the coastal plain does not extend beyond 30km inland where it is bounded by mountain ranges, including Bellenden Ker range with Queensland's highest peak (Bartle Frere 1,622m).

During the past 50 years the coastal plain between Tully and Cooktown has undergone major urban, rural residential and agricultural development. Total human population between Tully and Cooktown is 168,855 (Cook et al., 1997), 76% (128,022 people) living in Cairns (Centre for Applied Economic Research and Analysis, 1997). In addition to Tully, Cairns and Cooktown, other human population centres are Mission Beach/Innisfail (Johnstone Shire) and Port Douglas/Mossman areas (Douglas Shire). North of Cooktown, population density is low and centres are sparse.

There are 10 major waterways between Tully and Cooktown (south to north): Hull R, Maria Ck, Moresby R, Johnstone R, Russell/Mulgrave R, Trinity Inlet, Barron R, Daintree R, Annan R and Endeavour R. Only one species of crocodile (*C. porosus*) inhabits this area, and tidal

waterways comprise most of its habitat. Six flow through towns or cities: Hull R (Tully); Johnstone R (Innisfail); Russell/Mulgrave R, Trinity Inlet, Barron R (Cairns); and Endeavour R (Cooktown).

METHODS

We surveyed the major waterways between Tully and Cooktown for Estuarine Crocodiles from June 1996 to May 1998. Surveys were conducted by spotlighting from a small motorboat at night within 3 hours each side of low tide. Tidal reaches of waterways were surveyed, including adjacent freshwater sections passable by small motorboat. Total length of each crocodile was estimated and recorded in size classes: 0.2-0.4m (hatchling/yearling), 0.5-1.0m, 1.1-2.0m, 2.1-3.0m, 3.1-4.0m and 'eyes only' (crocodile sighted only by eye shine). Locations of crocodiles were determined by global positioning systems and topographic maps. We compare our data to surveys by Taplin (1987) and Kreiger & Fell (1991). However, we are unable to make statistical comparison.

Surveys were conducted to international standards (Bayliss, 1987; Kofron, 1992) with recognition of inherent weaknesses (Webb & Smith, 1987). For example, wariness in crocodiles is a function of size (Webb & Messel, 1979), older and larger crocodiles being more 'wary' and thus difficult to detect. However, we surveyed tidal rivers, which relative to other aquatic habitats (e.g. vegetated swamps) are easy to survey. In such areas a higher proportion of total number of crocodiles present is seen (Webb et al., 1987). Following convention, we define density as number of crocodiles observed per kilometre of waterway, excluding hatchlings and yearlings. Distance of a waterway from Cairns is measured from the central business district for this study.

RESULTS AND DISCUSSION

We sighted 146 crocodiles in 346km of waterway (Table 1): 0.2-0.4m ($n = 29$), 0.5-1.0m (23), 1.1-2.0m (41), 2.1-3.0m (19), 3.1-4.0m (10) and eyes only (24). Crocodile densities in river systems were 0.11/km to 1.00/km. Overall crocodile density in waterways between Tully and Cooktown was 0.34/km.

HULL RIVER. Hull R system is east of Tully with a catchment area of 12,996ha (Russell & Hales, 1997), originating in Walter Hill Range to the west (highest peak 1,068m) and draining a

TABLE 1. Results of spotlight surveys of Estuarine Crocodiles (*Crocodylus porosus*) in major waterways between Tully and Cooktown from June 1996 to May 1998. Density is number of crocodiles sighted per kilometre of waterway, excluding hatchlings and yearlings (0.2-0.4m total length).

Waterway	km Surveyed	No. of Crocs	Estimated Lengths					Eyes only	Density
			0.2-0.4m	0.5-1.0m	1.1-2.0m	2.1-3.0m	3.1-4.0m		
Hull River	38	21	12	0	3	3	2	1	0.24
Maria Creek	17	2	0	1	1	0	0	0	0.12
Moresby River	44	6	0	0	3	0	0	3	0.14
Johnstone River	41	7	1	3	3	0	0	0	0.15
Russell/Mulgrave R	63	9	2	2	4	0	1	0	0.11
Trinity Inlet	40	20	0	4	10	3	0	3	0.50
Barron River	22	7	0	0	2	3	2	0	0.32
Daintree River	25	21	6	8	4	0	0	3	0.60
Annan River	12	12	0	1	2	4	2	3	1.00
Endeavour River	44	41	8	4	9	6	3	11	0.75
Total	346	146	29	23	41	19	10	24	0.34

narrow coastal plain. Hull R and North Hull R are the major waterways, converging 2km from the coast into an estuary. Hull R flows through Hull R National Park (3,070ha) immediately adjacent to the coast.

The catchment is 76% forested, almost all in Wet Tropics World Heritage Area, and 14% under agriculture (sugarcane). Mangrove (1,326 ha), other swamp forest (81ha, predominantly *Melaleuca*) and rainforest comprise the existing natural vegetation. Although the only urban centre is the township Hull Heads (Russell & Hales, 1997), the Hull R system is heavily used for recreational boating and fishing. Commercial gill netting occurs at low to moderate level.

We surveyed 38km on 5-7 April 1997, sighting 21 crocodiles at 0.24/km: 0.2-0.4m ($n = 12$), 1.1-2.0m (3), 2.1-3.0m (3), 3.1-4.0m (2) and eyes only (1). Two nests were sighted.

MARIA CREEK. Maria Ck system is a group of small coastal streams 100km S of Cairns originating in Walter Hill Range to the west and draining a narrow coastal plain. It flows through Maria Ck National Park (749ha) immediately adjacent to the coast and in Wet Tropics World Heritage Area. Catchment area is 24,642ha, 49% cleared predominantly for agriculture (sugarcane; Russell & Hales, 1997). The main waterway is 25km long with a relatively large estuary, sheltered and lengthened by a sandspit extending south from Kurrimine Beach. Half of the national park is mangrove (350ha), the remainder other swamp forest and rainforest (Australian Nature Conservation Agency, 1996).

Maria Ck National Park is an important wetland in Australia. Maria Ck system is heavily used for recreational boating and fishing, and commercial gill netting occurs at low level. High levels of nutrients and sediments in runoff from adjacent agricultural lands may be impacting on the wetlands (Australian Nature Conservation Agency, 1996). Catchment area contains El Arish, Mission Beach and Kurrimine townships.

We surveyed 17km on 4-5 April 1997, sighting two crocodiles: 0.5-1.0m ($n = 1$) and 1.1-2.0m (1). Density was 0.12/km.

MORESBY RIVER. Moresby R system is 80km south of Cairns, a wetland 24km long and 12km wide, mostly in Wet Tropics World Heritage Area. Catchment area is 126km², 48% remaining as natural vegetation, and with a population of 300 (Eyre & Davies, 1996). Moresby R communicates with the Coral Sea through a restricted passage in Moresby Range, with a broad sheltered estuary west of the range. The southern system is bounded to the east by a series of sand dunes. The tidal reach of Moresby R is 20km long with headwaters in Basilisk Range, a low range in the western coastal lowlands. Natural vegetation is mangrove, other swamp forest and rainforest, and the estuary contains significant seagrass beds. Moresby R system is an important wetland in Australia (Australian Nature Conservation Agency, 1996).

Coastal lowlands north, south and west of Moresby R system have undergone extensive clearing for agriculture (sugarcane). Mourilyan Harbour, at northern end of the estuary and sheltered by Moresby Range, loads sugar onto

sea-going vessels. Moresby R is heavily used for recreational fishing and boating, and commercial gill netting occurs at low level.

We surveyed 44km on 31 January to 4 February 1997, sighting six crocodiles: 1.1-2.0m ($n = 3$) and eyes only (3). Density was 0.14/km.

JOHNSTONE RIVER. North Johnstone R (125km) and South Johnstone R (90km) are the main waterways of Johnstone R system 64km south of Cairns, originating on Atherton Tableland and flowing through vast rainforest on the eastern escarpment of Bellenden Ker Range. Catchment area is 163,050ha (population 17,860; Eyre & Davies, 1996): 54% rainforest, predominantly on slopes; 38% under agriculture (cattle, sugar cane, bananas), rural residential and urban uses, predominantly in coastal lowlands and Atherton Tableland; and 8% mangrove and other swamp forest (Pitts, 1993). Along the lower river system much clearing has occurred to very edge of the stream bank.

North Johnstone R is 43km long in the coastal plain, and South Johnstone R 31km. The two rivers converge at Innisfail forming Johnstone R estuary 5km long. Johnstone R flows through centre of Innisfail, population 8,987 (Cook et al., 1997). Innisfail is home for a commercial fishing fleet, and the river is also heavily used for recreational boating and white-water rafting. Johnstone R has been closed to commercial gill netting for 30-40 years.

We surveyed 41km on 10-12 January 1997, sighting 7 crocodiles at 0.15/km: 0.2-0.4m ($n = 1$); 0.5-1.0m (3); 1.1-2.0 (3). Johnstone R system (11km) was surveyed previously in 1986 (Taplin, 1989), 6 crocodiles sighted at 0.55/km: 0.5-1.8m ($n = 2$), 1.9-3.0m (3) and eyes only (1). Densities are low and show no increase.

RUSSELL/MULGRAVE RIVERS. Russell R and Mulgrave R flow through agricultural and rural residential lands of south Cairns, headwaters in mountains to the west. The lower river system is in a narrow plain between Bellenden Ker Range and Graham Range/Malbon Thompson Range to the east coastally. Russell R flows northeast and Mulgrave R southeast. The two rivers converge 1km from the sea to form Mutchero Inlet, a constricted passage through submerged parts of Graham Range to the south and Malbon Thompson Range to the north. Catchment area of Russell R is 57,000ha, and Mulgrave R 145,000ha (Australian Nature Conservation Agency, 1996).

Surrounding natural vegetation is mangrove, other swamp forest and rainforest, although most floodplain in coastal lowland has been cleared. Forty-eight percent of the catchment area remains in natural state and is Wet Tropics World Heritage Area; and 27% is under agriculture (sugarcane). Russell R flows through Russell R National Park (4,100ha), an important wetland in Australia (Australian Nature Conservation Agency, 1996). Tidal sections of the Russell/Mulgrave R are heavily used for recreational fishing and boating, and adjacent freshwater sections for swimming and rafting. The rivers have been closed to commercial gill netting for more than 10 years.

We surveyed 63km (Russell R 38km, Mulgrave R 25km) 18-21 January 1997, sighting 9 crocodiles at 0.11/km: 0.2-0.4m ($n = 2$), 0.5-1.0m (2), 1.1-2.0m (4) and 3.1-4.0m (1). One problem crocodile (1.9 m) was removed from Mulgrave R during the study because it was in a freshwater swimming area. Russell/Mulgrave R (27km) were surveyed previously in 1991 (Kreiger & Fell, 1991), seven crocodiles sighted at 0.26/km: 0.5-1.0m ($n = 1$), 1.1-1.8m (2) and eyes only (4). Also, 24km were surveyed in 1984 (Taplin, 1989), 2 crocodiles sighted at 0.04/km: 0.2-0.4m ($n = 1$) and eyes only (1). Densities are consistently low and show no increase.

TRINITY INLET. Trinity Inlet is 18km long by 6km wide in north-south direction, comprising 6,475ha: mangrove 3,600ha, seagrass 1,000ha, open water 940ha, tidal flats 900ha, salt flats 20ha, freshwater swamp 10ha and sand ridge 5ha. Catchment area is 30,000ha. Trinity Inlet is a blind estuary, previously the mouth of Mulgrave R whose communication with the sea has shifted south (Australian Nature Conservation Agency, 1996).

Cairns surrounds Trinity Inlet: Cairns Port at its mouth; urban development and industry on its western side; and rural residential and agriculture on its southern and eastern sides. Most of the previously fringing freshwater swamp forest has been cleared. The system is heavily used for recreational fishing and boating, and also by large sea-going vessels; commercial gill netting occurs at extremely high level. Despite proximity to a major population centre, the ecosystem is intact and overall water quality good (Australian Nature Conservation Agency, 1996).

We surveyed 40km on 7-9 and 20 May 1998, sighting 20 crocodiles at 0.50/km: 0.5-1.0m ($n = 4$), 1.1-2.0 (10), 2.1-3.0 (3) and eyes only (3).

Also, we previously surveyed 40km of Trinity Inlet on 18 April and 19 May 1997, sighting 13 crocodiles at 0.33/km: 0.5-1.0m ($n=2$), 1.1-2.0m (4), 2.1-3.0m (5), 3.1-4.0m (1) and eyes only (1). Although we sighted no hatchlings, Keith Cook (Cairns Crocodile Farm, pers. comm) observed one in 1997. In addition, courtesy Mark Read (Queensland Parks and Wildlife Service), we searched for nests by helicopter on 21 February 1998 but sighted none. Two problem crocodiles were removed during the study: one (3.1m) from Chinaman's Ck (February 1998) that attacked a teenage girl, and a second (1.5m) from the same drain in April. Trinity Inlet (55km) was surveyed previously in 1991 (Kreiger & Fell, 1991), seven crocodiles sighted at 0.13/km: 0.5-1.0m ($n=1$), 1.1-1.8m (2) and eyes only (4). Densities are consistently low and show no increase.

BARRON RIVER. Barron R is one of the longest easterly-flowing rivers (165km) in Cape York Peninsula, with headwaters in Atherton Tableland at 1234m elevation (North Queensland Joint Board, 1997). It breaches Macalister/Lamb Ranges through a major gorge (6km length) then forms a delta (50km²) in the narrow coastal plain (8km wide). Barron R flows through Cairns just north of the urban centre, Machan's Beach community at its mouth. Catchment is 200,000ha, population 42,000.

Natural vegetation along lower Barron R is mangrove, other swamp forest and rainforest, most cleared for sugarcane and residential land use. A significant area of mangrove (6km²) remains at the mouth. Queensland Government (Department of Primary Industries, 1993) is concerned about catchment condition, particularly erosion, weeds, urban expansion, nutrient enrichment, impacts on wildlife and loss of wetlands. Tidal section of the river is heavily used for recreational fishing and boating, and adjacent freshwater section for swimming and rafting. Commercial gill netting occurs at low level.

We surveyed 22km (tidal reaches) on 4-6 May 1998, sighting seven crocodiles at 0.32/km: 1.1-2.0m ($n=2$), 2.1-3.0m (3) and 3.1-4.0m (2). Also, we surveyed the same tidal reaches previously 28-29 June 1996, sighting seven crocodiles at 0.32/km: 0.5-1.0m ($n=1$), 1.1-2.0m (1) and 2.1-3.0m (5). Densities are consistently low. Two problem crocodiles (2.6m each) were removed during the study, one from Richters Ck (29 January 1997) frequenting swimming beaches and one from Thomatis Ck (9 December

1997) that attacked a swimmer at Yorkey's Knob Beach.

DAINTREE RIVER. Daintree R (120km length) is 78km northwest of Cairns, headwaters in Great Dividing Range. Catchment is 2125km², 90% in Wet Tropics World Heritage Area and most protected in Daintree National Park and Dagmar Range National Park, population 1000. Rainforest comprises 74% of catchment, originally 90%. The estuary is 5km long, tidal influence extending 24km upstream. The lower 13km of Daintree R, up to 10km wide with mangrove and other swamp forest, is an important wetland (Australian Nature Conservation Agency, 1996; Eyre & Davies, 1996).

Daintree R in the coastal lowlands occupies a narrow valley between Thornton Range to the north and Dagmar Range to the south. One-half (16,400ha) of this floodplain is cleared for sugarcane (12,000ha) and cattle (4,400ha), the other half (17,300ha) remaining as mangrove, other swamp forest and rainforest (Burrows, 1998). Mangrove is most extensive at river mouth to 6km upstream. Daintree R is heavily used for recreational boating, and also commercial boating for wildlife tours. The river was closed to commercial gill netting about 12 years ago.

We surveyed 25km (starting 7km above river mouth at ferry crossing) on 5 September 1997, sighting 21 crocodiles: 0.2-0.4m ($n=6$), 0.5-1.0m (8), 1.1-2.0m (4) and eyes only (3). Density was 0.60/km, however fog made visibility poor. One crocodile (2.4m) that attacked a dog was removed during the study (8 May 1997). Daintree R (31km) was surveyed previously by Kreiger & Fell (1991), 27 crocodiles sighted at 0.85/km: 0.2-0.4m ($n=1$), 0.5-1.0m (17), 1.1-1.8m (3), 1.8-4.0m (3) and eyes only (3). Also, Taplin (1989) surveyed 21km in 1984, sighting 16 crocodiles at 0.75/km: 0.5-1.8m ($n=9$), 1.9-3.0m (2) and eyes only (5). Densities are consistently low and show no increase.

Also in Douglas Shire during the study, 1 problem crocodile (1.8m) was removed at Wonga Beach (7km south of Daintree R); 2 (3.4m each) from Mossman R (17km south of Daintree R); 29 January and 23 March 1998) that took dogs; and 1 (2.1m) from Bloomfield R (41km north of Daintree R, 10 February 1998).

ANNAN RIVER. Annan R is 6km south of Cooktown and is least disturbed of the major

waterways. Catchment is 750km², with population 300 (Eyre & Davies, 1996). Ninety percent of catchment retains natural vegetation (40% rainforest, predominantly upper half; 40% dry *Eucalyptus* woodland, predominantly lower half), and 10% cleared for cattle. The tidal section is bounded immediately by mangrove, other swamp forest and rainforest. The estuary is 6km length. Recreational boating occurs at low to moderate level in the tidal section, and commercial gill netting at moderate level.

We surveyed 12km (tidal reaches) on 9-10 October 1997, sighting 12 crocodiles at 1.00/km: 0.5-1.0 ($n=1$), 1.1-2.0 (2), 2.1-3.0 (4), 3.1-4.0 (2) and eyes only (3). Annan R (11km) was surveyed previously by Kreiger & Fell (1991), sighting six crocodiles at 0.55/km: 1.9-4.0m ($n=1$) and eyes only (5). Densities are low but may indicate a slight increase.

ENDEAVOUR RIVER. Endeavour R system has two major channels: Endeavour R flowing west to east, and Endeavour R Right Branch north to south. Cooktown is on the southern banks of Endeavour R at its mouth, population 1411 (Cook et al., 1997). Cooktown McIvor River Rd parallels Endeavour R for 30km near Cooktown, and adjacent land is under rural residential use and agriculture (peanuts, corn, bananas); however only little clearing has encroached to the banks of Endeavour R. Vegetation along Endeavour R Right Branch remains predominantly natural.

The estuary is 5km long, its upper half in Endeavour R National Park (2,170ha). Endeavour R is 500m wide at its mouth, narrowing to 100m at junction with Endeavour R Right Branch 11km upriver. Vegetation in the tidal area is mangrove; along freshwater sections of the river, rainforest; and along freshwater creeks, *Melaleuca* swamp. Recreational boating occurs at moderate level. The river was closed to commercial gill netting about 30 years ago.

We surveyed 44km on 14-16 September 1997, sighting 41 crocodiles at 0.75/km: 0.2-0.4m ($n=8$), 0.5-1.0m (4), 1.1-2.0m (9), 2.1-3.0m (6), 3.1-4.0m (3) and eyes only (11). Two crocodiles (3.7m, 3.8m) frequenting Cooktown wharf were removed during the study. Endeavour R system (28km) was surveyed previously by Kreiger & Fell (1991), sighting 28 crocodiles at 0.96/km: 0.2-0.4m ($n=5$), 0.5-1.0m (16), 1.1-1.8m (1), 1.9-4.0m (2) and eyes only (4). Densities are consistently low and show no increase.

MANAGEMENT CONSIDERATIONS

Densities of Estuarine Crocodiles in waterways between Tully and Cooktown range from 0.11/km to 1.00/km. In total, we surveyed 346km of waterway between Tully and Cooktown, sighting 146 crocodiles at overall density 0.34/km. Previously Kreiger & Fell (1991) surveyed five waterways, sighting crocodiles at overall density 0.45/km. In these five waterways we sighted crocodiles at density 0.47/km. Also, Taplin (1989) surveyed 3 waterways in 1984-1986, sighting crocodiles at overall density 0.41/km. In these 3 waterways we sighted crocodiles at overall density 0.22/km. The densities are consistently low and show no increase.

Overall crocodile density between Tully and Cooktown (0.34/km) is low relative to most waterways on Cape York Peninsula: 0.7/km, rivers in Lakefield National Park (165km northwest of Cooktown; Read & Miller, 1998); 5.9/km and 10.5/km, Wenlock R and Tentpole Ck (northwest tip of Cape York Peninsula), respectively (Read, 1998); and 0.3/km to 3.6/km, other rivers on western Cape York Peninsula (Read, 1998). In the Northern Territory, Estuarine Crocodile populations are recovering, with mean annual rate of increase 2-3% reported in several rivers (Webb et al., 1987) and overall annual rate of population increase 8% (Bayliss, 1987).

Estuarine Crocodiles nest in the wet season, and flooding is a major threat to egg survival. In the Northern Territory, mean egg survivorship is 25%, inundation of nests the major cause of mortality (Webb et al., 1987). In some areas flooding accounted for 100% egg mortality.

No effort was made to locate nests except for one helicopter search of Trinity Inlet, but none was seen. However, 2 nests were observed near the Hull R, and 1 near the Bloomfield R subsequently inundated (Tony Frisby, Queensland Parks and Wildlife Service, pers. comm.). In addition, hatchlings/yearlings were seen in several rivers: Hull R (12), Johnstone R (1), Russell/Mulgrave R (2), Trinity Inlet (1, Keith Cook, Cairns Crocodile Farm, pers. comm.), Daintree R (6) and Endeavour R (8). There was no evidence of nesting in Maria Ck, Moresby R, Barron R, Mossman R or Annan R. In total, 30 hatchlings/yearlings were observed in 346km of waterway, which is a low number.

Crocodile densities in tidal rivers are partly a function of proximity to successful nesting areas.

For example in the Northern Territory, Webb et al. (1987) observed crocodiles at density 3.2/km in tidal rivers with successful nesting areas, and 0.7/km without. We attribute the low number of hatchlings/yearlings between Tully and Cooktown to negative impacts of human activities, largely preventing successful nesting.

Extensive deforestation and development in the catchment of some rivers probably effect greater rises in water levels than occurred previously, partially accounting for the paucity of successful nesting. In addition, many river banks previously available for nesting are now cleared to water's edge, and disturbance by motor boats may also discourage nesting. The human population and agricultural development were identified previously as causing significant degradation of crocodile habitat between Tully and Cooktown (Taplin, 1987). Further, Taplin (1987) referred to this crocodile population as depleted', with only small numbers at low densities.

There are 16 protected areas with crocodile habitat between Tully and Cooktown. They range from 6ha to 76,000ha. Daintree National Park is the largest, however it encompasses predominantly Great Dividing Range and lowland rainforest, with relatively little crocodile habitat. The next 3 largest are Cedar Bay National Park (5,650ha), Russell R National Park (4,100ha) and Ella Bay National Park (3,710ha). The fifth largest is Hull R National Park (3,070ha) and almost all crocodile habitat (waterway, mangrove, swamp forest). Crocodiles are at low density here too, 0.24/km.

Estuarine Crocodiles are highly mobile, and probably no protected area between Tully and Cooktown contains sufficient habitat for the life cycle. Taplin (1987) believed adult crocodiles moved in and out of protected areas, juveniles and subadults dispersing into surrounding non-protected areas. Commercial gill netting in tidal rivers was identified as a major threatening factor to crocodiles (Taplin, 1987), but the impact remains to be quantified. This activity continues in six major waterways between Tully and Cooktown. Johnstone, Russell/Mulgrave, Daintree and Endeavour Rivers are closed to this fishing.

Despite low densities, problem crocodiles are not infrequent in the study area, often as a result of human behaviour, such as discarding fish scraps at public facilities (boat ramp, wharf, jetty). Two crocodile attacks occurred in Cairns

during the study, and public perception is now that large numbers of crocodiles occur between Tully and Cooktown. However many people use these waterways daily, usually without incident, and consequently some crocodiles may be coming less wary and also more visible. Twelve problem crocodiles were removed during the study: 2 had attacked humans, 2 from swimming areas, 3 had attacked dogs, 2 frequented a wharf and 3 were otherwise threats to humans. Removed crocodiles measured 1.1-2.0m ($n = 3$), 2.1-3.0m (4) and 3.1-4.0m (5).

In the interests of public safety, the Queensland Parks and Wildlife Service initiated a Trial Intensive Management Area for Crocodiles in May 1998. This 3-year trial program targets all crocodiles for removal in designated areas near Cairns, Port Douglas and Mossman. Also, an education program provides information on appropriate and safe behaviour in crocodile habitat. Research is focussed on surveys and on-going monitoring. The survey data presented here precede implementation of the crocodile removal zone and comprise baseline data for comparison against future surveys.

CONCLUSIONS

Contrary to public perception, the crocodile population between Tully and Cooktown exists at low density, showing no increase over 14 years. Human activities such as urban, rural residential and agricultural development, clearing of riparian vegetation, disturbance by motor boats, commercial gill netting in estuaries, and removal of crocodiles appear to be keeping crocodile numbers low.

ACKNOWLEDGEMENTS

The following people rendered assistance: Angela Chapman, Tony Frisby, Ian King, Gordon LaPrak, Jeffrey Miller, Frank Nissan, Richard Orchard, Mark Read, Rupert Russell, Clay Smith, Willie Smith, Laurie Taplin and Brent Vincent.

LITERATURE CITED

- AUSTRALIAN NATURE CONSERVATION AGENCY 1996. A directory of important wetlands in Australia. 2nd edn. (ANCA: Canberra).
- BAYLISS, P. 1987. Survey methods and monitoring within crocodile management programmes. Pp. 157-175. In Webb, G.J.W., Manolis, S.C. & Whitehead, P.J. (eds) Wildlife management: crocodiles and alligators. (Surrey Beatty & Sons: Sydney).

- BUREAU OF METEOROLOGY 1975. Climatic averages: Australia. (Australian Government Publishing Service: Canberra).
1977. Rainfall statistics: Australia. (Australian Government Publishing Service: Canberra).
- BURROWS, D.W. 1998. Far North Queensland 2010 Regional Environment Strategy: Key Waterways Report. (James Cook University of North Queensland: Townsville). [Draft report].
- CENTRE FOR APPLIED ECONOMIC RESEARCH AND ANALYSIS 1997. Report on the Cairns Regional Economy. (Australian Economic Consultants Group: Townsville).
- COOK, T., GILLAM, E., BARKER, R. & WARD, G. 1997. Recent Population and Housing Trends in Queensland 1997. (Queensland Department of Local Government and Planning: Brisbane).
- DEPARTMENT OF ENVIRONMENT AND HERITAGE 1994. Nature Conservation Act 1992. (Government Printer: Brisbane).
- DEPARTMENT OF PRIMARY INDUSTRIES 1993. The Condition of River Catchments in Queensland: A Broad Overview of Catchment Management Issues. (Department of Primary Industries [ICM]: Brisbane).
- EYRE, B. & DAVIES, P. 1996. A preliminary assessment of suspended sediment and nutrient concentrations in three Far North Queensland catchments. Pp. 57-64. In Hunter, H.M., Eyles, A.G. & Rayment, G.E. (eds) Downstream effects of land use. (Department of Natural Resources: Brisbane).
- GROOMBRIDGE, A. 1987. The distribution and status of world crocodilians. Pp. 9-21. In Webb, G.J.W., Manolis, S.C. & Whitehead, P.J. (eds) Wildlife management: crocodiles and alligators. (Surrey Beatty & Sons: Sydney).
- HERBERT, B. & PEETERS, J. 1995. Freshwater fishes of Far North Queensland. (Department of Primary Industries: Brisbane).
- KOFRON, C.P., 1992. Status and habitats of the three African crocodiles in Liberia. *Journal of Tropical Ecology* 8: 265-273.
- KREIGER, G. & FELL, D. 1991. Results from Population Survey of Crocodiles on the North, East Coast Of Queensland — February and June 1991. (Queensland Parks and Wildlife Service: Cairns). [Unpublished internal report].
- MESSEL, H., VORLICEK, G.C., WELLS, A.G. & GREEN, W.J. 1981. Surveys of tidal river systems in the Northern Territory of Australia and their crocodile populations. Monograph No. 1. (Pergamon Press: Sydney).
- NORTH QUEENSLAND JOINT BOARD 1997. Barron River Catchment Rehabilitation Plan: Technical Report on Rehabilitation Needs. (North Queensland Joint Board: Cairns).
- PITTS, D. 1973. Water quality management in the Johnstone River catchment. Pp. 1-43. In Resource Assessment Commission (commissioned by) Water quality management: five case studies. (Resource Assessment Commission: Canberra).
- READ, M. 1998. Report on Distribution and Abundance of the Estuarine Crocodile (*Crocodylus porosus* Schneider) in Queensland. 3. Western and Northwestern Cape York Peninsula. Research Conducted October-November 1997. (Department of Environment and Heritage: Townsville). [Unpublished internal report].
- READ, M. & MILLER, J.D. 1998. Report on Distribution and Abundance of the Estuarine Crocodile (*Crocodylus porosus* Schneider) in Queensland. 2. Lakefield National Park. Research Conducted September 1997. (Department of Environment: Townsville). [Unpublished internal report].
- ROSS, J. P. (ed.) 1998. Crocodiles. Status Survey and Conservation Action Plan. 2nd edn. (IUCN: Gland).
- RUSSELL, D.J. & HALES, P.W. 1997. Fish Resources and Stream Habitat of the Liverpool, Maria and Hull Catchments. (Queensland Department of Primary Industries: Brisbane).
- TAPLIN, L.E. 1987. The management of crocodiles in Queensland, Australia. Pp. 129-140. In Webb, G.J.W., Manolis, S.C. & Whitehead, P.J. (eds) Wildlife management: crocodiles and alligators. (Surrey Beatty & Sons: Sydney).
1989. Crocodile Management Plan 1989. (Department of Environment and Heritage: Townsville). [Unpublished internal report].
- WALSH, B. & WHITEHEAD, P.J. 1993. Problem crocodiles, *Crocodylus porosus*, at Nhulunbuy, Northern Territory: an assessment of relocation as a management strategy. *Wildlife Research* 20: 127-135.
- WEBB, G.J.W. & MESSEL, H. 1979. Wariness in *Crocodylus porosus*. *Australian Wildlife Research* 6: 227-234.
- WEBB, G.J.W. & SMITH, M.A. 1987. Life history parameters, population dynamics and the management of crocodilians. Pp. 199-210. In Webb, G.J.W., Manolis, S.C. & Whitehead, P.J. (eds) Wildlife management: crocodiles and alligators. (Surrey Beatty & Sons: Sydney).
- WEBB, G.J.W., WHITEHEAD, P.J. & MANOLIS, S.C. 1987. Crocodile management in the Northern Territory of Australia. Pp. 107-124. In Webb, G.J.W., Manolis, S.C. & Whitehead, P.J. (eds) Wildlife management: crocodiles and alligators. (Surrey Beatty & Sons: Sydney).

SPONDYLIDS FROM THE MEDITERRANEAN SEA AND ATLANTIC OCEAN (MOLLUSCA: BIVALVIA: SPONDYLIDAE)

KEVIN LAMPRELL, JOHN STANISIC AND PETER CLARKSON

Lamprell, K., Stanisic, J. & Clarkson, P. 2001 06 30: Spondylids from the Mediterranean Sea and Atlantic Ocean (Mollusca: Bivalvia: Spondylidae). *Memoirs of the Queensland Museum* 46(2): 611-622. Brisbane. ISSN 0079-8835.

A new spondylid from the Ligurian Sea, *Spondylus cevikeri* sp. nov., is described. A spondylid from the Cape Verde Islands, possibly new and very similar to the Indo-Pacific *Spondylus linguafelis* Sowerby, G.B. II, 1847 is recorded and figured. The numerous synonyms of *Spondylus gaederopus* Linnaeus, 1758, are discussed and additional taxonomic notes presented. *Spondylus reevei* Fulton, 1915 is shown to be valid; *Spondylus limbatus* Sowerby, G.B. II, 1847 is shown to be a prior name for *Spondylus calcifer* Carpenter, 1857; *Spondylus powelli* Smith, 1892 is shown to be a junior synonym of *Spondylus senegalensis* Schreibers, 1793; *Spondylus multisetosus* Reeve, 1856 previously known only from the Indo-Pacific is now recorded from the Mediterranean Sea; *Spondylus lamarcki* Chenu, 1845, is placed in synonymy with *Spondylus spinosus* Schreibers, 1793; and variations of *S. spinosus*, including an all-brown specimen, are discussed and figured. □ *Spondylus*, new species, Mediterranean Sea, Atlantic Ocean.

Kevin Lamprell & John Stanisic, Queensland Museum, PO Box 3300, South Brisbane 4101;
Peter Clarkson, PO Box 713, Port Lincoln 5606; 8 May 2000.

Spondylids are an extremely difficult group to identify by shell characters because of the high level of intraspecific variability related to growth pattern. In part of their life cycle all spondylids are attached to the substrate by the lower (right valve), at least vestigially. In some species, such as *Spondylus imperialis* Chenu, 1845, *S. pratti* Parth, 1998 or *S. regius* Linnaeus, 1758, the right and lvs are virtually mirror images of each other in terms of spination, because the right valve grows free of the substrate in adulthood. However, in the majority of species the area of attachment of the right valve is widely variable and, to some extent, the shell will mould itself to the shape of its anchorage. If they become dislodged due to wave action or some other reason, the ornamentation of the right valve will be further affected. As such, there may be little consistency in the overall shape and ornamentation of the right valve. This leaves only the top (left) valve and internal features of the shell as useful characters for field identifications. Because of the intraspecific variability of many species, such as *S. gaederopus* Linnaeus, 1758, a wide range of specimens may be necessary in order to establish accurate identification.

Reasonably reliable taxonomic characters appear to be: width of ears (auricles); inflation of left (top) valve; inflation of right (lower) valve; number and structure of ribs; ornamentation (sculpture) of ribs; sculpture of interstitial areas; external colour (in some species); internal shell

colour particularly the colour of the internal margin crenulations. Problems of identification could be solved by molecular studies, sperm ultrastructure or scanning electron microscopy, and some species may yet be reduced to subordinate rank by the use of such methods. However, these tests are laboratory-based and do not help the field worker with identification of species.

The authors have had the opportunity to study spondylids from the Mediterranean Sea, the Senegal coast, Cape Verde and Canary Islands including several variations of the extremely variable *S. gaederopus*. The various synonyms (forms) of this species are discussed and a new species, *S. cevikeri*, is described. Additional taxonomic notes are also presented on several other spondylids.

ABBREVIATIONS. AMS, Australian Museum, Sydney; QM, Queensland Museum, Brisbane; DC coll, Dogan Ceviker collection; FS coll, Frank Swinnen collection; KL coll, Kevin Lamprell collection; NSW, New South Wales; Qld, Queensland; pv, paired valves; rv, right or upper valve; lv, left or lower valve.

MEASUREMENT DETAILS. Height = greatest vertical distance between the centre of the umbo and the lowest part of the ventral margin of lv, excluding spines; width = greatest horizontal distance between the anterior and dorsal margins of lv, excluding spines; depth of pv = greatest

distance between the external surfaces of the left and right valves excluding ribs and spines.

Family SPONDYLIDAE Gray, 1826

***Spondylus gaederopus* Linnaeus, 1758**
(Fig. 1)

Spondylus gaederopus Linnaeus, 1758: 1136; Schreibers, 1793: 152 (based on Chemnitz, 1784: 459); Chemnitz 1845: pl. 1, fig. 1; pl. 2, figs 1-2.4; Sowerby 1847, figs 29, 41; Reeve 1856: fig. 13; Fulton 1915: 331, sp. 1; Lucas 1978, 6-8; Abbott & Danee 1982: 317; Lamprell 1986: pl. 1, fig. 1a. *Spondylus mediterraneus* Hermann, 1781: 16. *Spondylus spinosus* Martyn, 1784 non Schreibers, 1793. *Spondylus inermis* Monterosato, 1875: 64. *Spondylus albinus* Monterosato, 1875: 64. *Spondylus coralinus* Monterosato, 1875: 64. *Spondylus foliosus* Monterosato, 1875: 64. *Spondylus uerileatus* Philippi, 1884: 74. *Spondylus lamellosus* Pallary, 1904: 52, 244. *Spondylus mixtus* Koch and Pallary, 1900: 48, 371. *Spondylus unicus* Jousseaume, 1927: 33, 307.

TYPE MATERIAL. LECTOTYPE: Linnaean Collection, London (Dodge, 1952), Mediterranean Sea.

DESCRIPTION. Shell ovate, almost equivalve, height to 90mm, rv deeper than lv. Sculpture variable, both valves usually with 8-9 ribs ornamented with irregular shaped spines that are hollow underneath, varying from spatulate to flat or sharp spines; interstices with dense small prickles. Colour of lv usually purple, rv white; some orange or all white specimens are also known. Internally the crenulations are moderately fine, purple on the lv and usually white on the rv.

DISTRIBUTION AND HABITAT. Mediterranean Sea; northwest African coast; attached to dead coral or rock amongst algae to at least 30m. Usually covered in a distinctive orange-red sponge that appears to grow only on *Spondylus* (P. Clarkson, pers. obs.).

REMARKS. In both the 1758 and 1767 editions of the 'Systema Naturae', Linnaeus gave the same brief description of *Spondylus gaederopus*: 'S. testa aubaurita spinosa ... Natum altera

longior, line plana, ac si arte aut abrasa fuisset' with the locality 'M. Mediterraneo, arce adhaerens scopulis'. Twenty-eight figures from 9 different authors were quoted for *S. gaederopus* in the 12th edition of Linnaeus' 'Systema Naturae'. It has been shown that many of these figures refer to a number of spondylids other than *S. gaederopus* so that the diagnosis of the species by Linnaeus must be considered a composite and therefore undefined (Dodge, 1952). Dodge (1952), however, recognised a specimen of *S. gaederopus* lodged in the Linnaean Collection, London as the Linnaean type specimen. This specimen, while unidentified, not only closely agrees with the few details of the original description, but also was one of only two spondylids present in the collection.

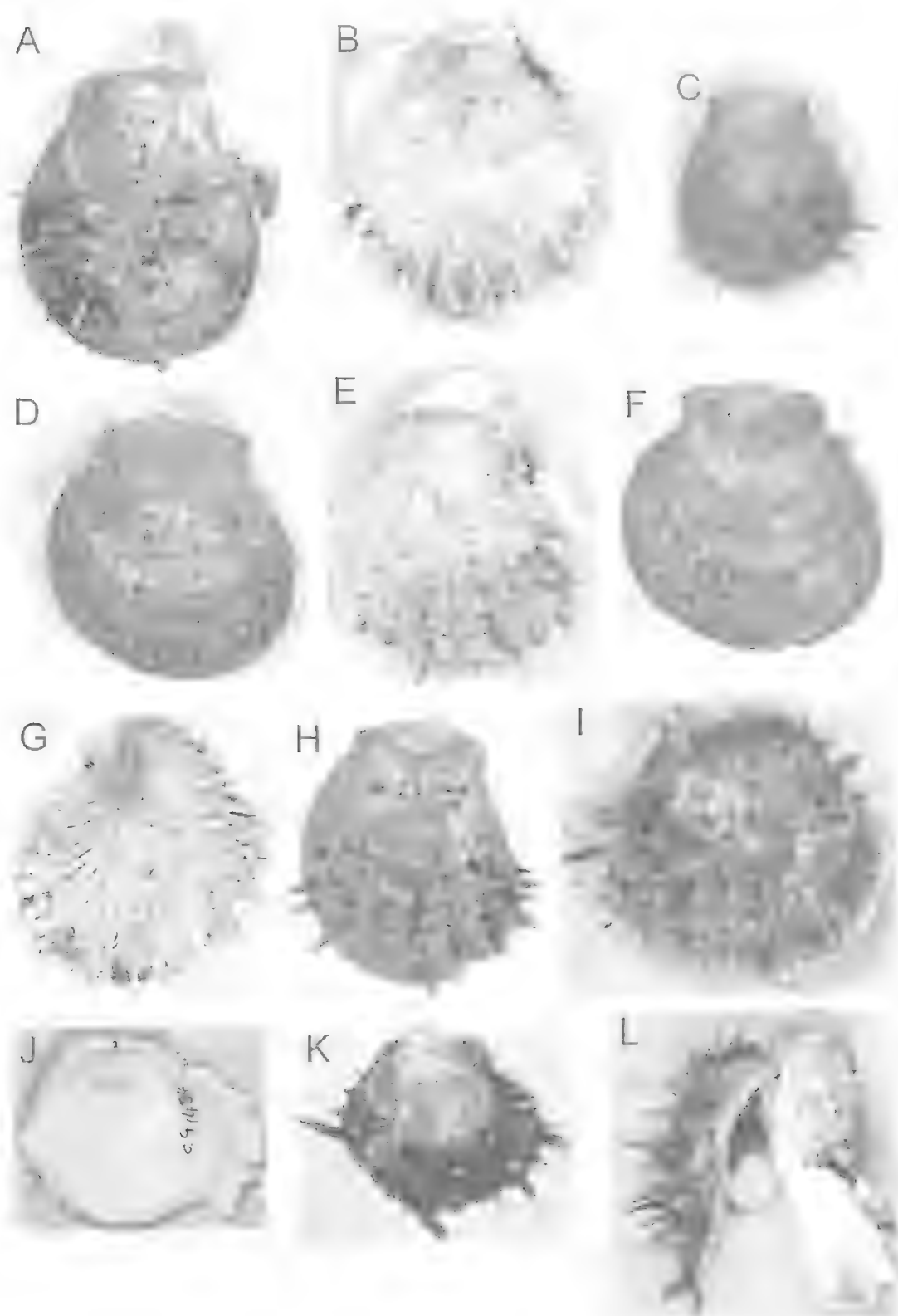
Numerous names have been used for the different forms of *S. gaederopus*. *S. spinosus* Martyn, 1784 non Schreibers, 1793 was introduced for specimens possessing sparse, long spines; *S. inermis* Monterosato, 1875 for specimens with sparse sculpture without strongly developed spines or other projections; *S. albinus* Monterosato, 1875 for white shelled forms; *S. coralinus* Monterosato, 1875 for coral red forms; *S. foliosus* Monterosato, 1875 for specimens with ornamentation of large, leaf-shaped radiating lamellae; *S. lamellosus* Pallary, 1904 for specimens with numerous spatulate lamellae; and *S. mixtus* Koch & Pallary, 1900 for specimens with numerous mixed, spatulate lamellae and spines. These names, while strictly synonyms of *S. gaederopus* have nevertheless proven useful when referring to the various forms of *S. gaederopus*.

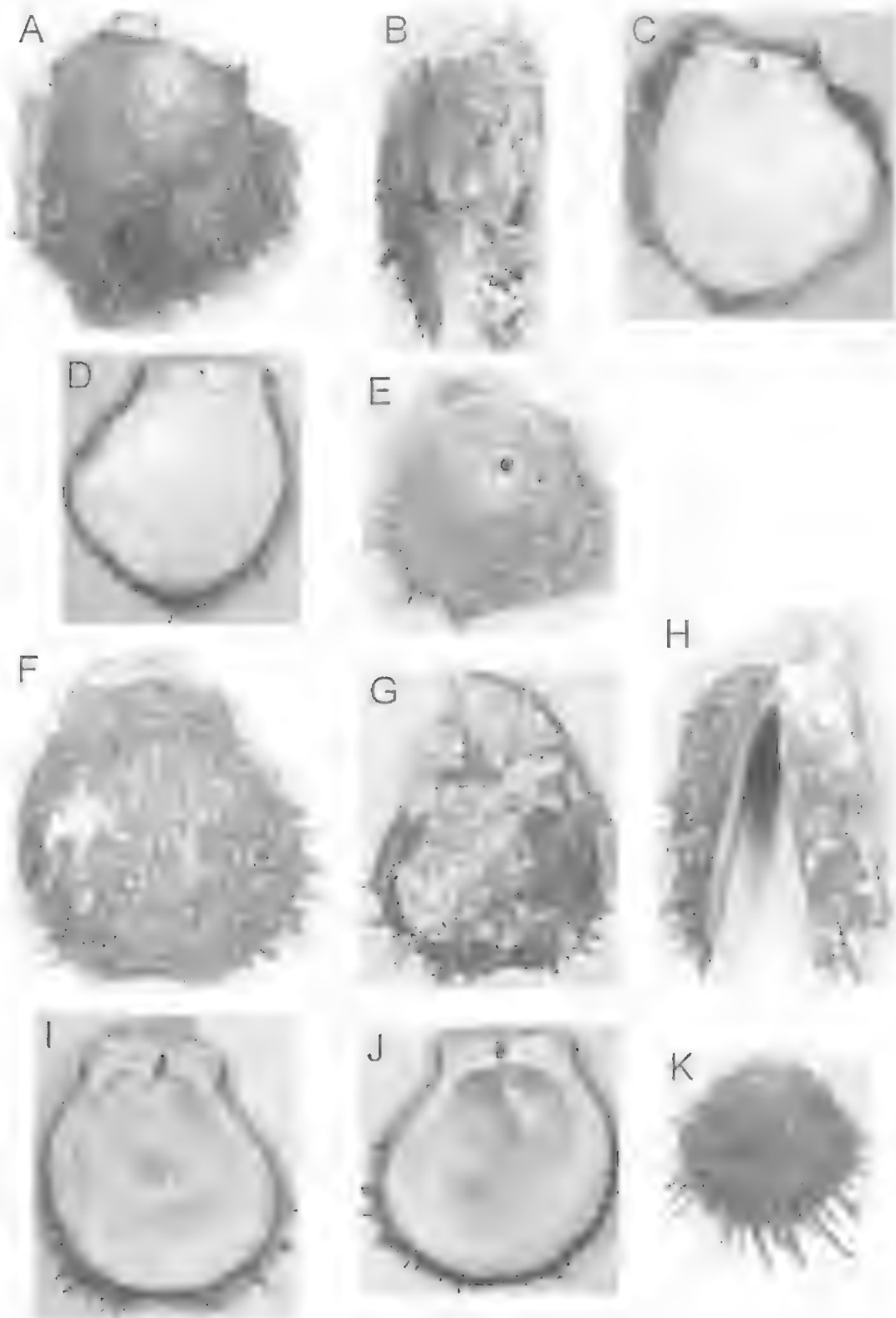
***Spondylus cevikeri* sp. nov.**
(Figs 2F-K, 3A-C)

ETYMOLOGY. Named for Dogan Ceviker (Istanbul).

MATERIAL. HOLOTYPE: AMS C204238. 1 pv. Ligurian Sea, height 80.7mm, width 76.5mm, depth of conjoined valves 43.1mm. **PARATYPES:** QMMO66960

FIG. 1. A-L. *Spondylus gaederopus* (Linnaeus). A, external view, lv, form *spinosus*, DC coll 209: height 71.3mm, width 60.0mm, depth of pv 32.0mm. B, external view, lv, form *mixtus*, FS coll: height 59.5mm, width 59.7mm, depth of pv 24.0mm. C, external view, lv, form *spinosus*, KL coll, Antibes 15.0m: height 40.02mm, width 34.5mm, depth of pv 22.5mm. D, external view, lv, form *inermis*, KL coll, Ligurian Sea, 45.0m: height 66.9mm, width 61.9mm, depth of pv 38.2mm. E, external view, lv, form *albinus*, KL coll, Majorca, Spain: height 49.5mm, width 42.5mm, depth of pv 32.5mm. F, external view, lv, form *coralinus*, DC coll 265: height 84.2mm, width 83.4mm, depth of lv 23.0mm. G, external view, rv, form *albinus*, DC coll, Karatas, Adana, 60-90.0m: height 44.2mm, width 36.6mm, depth of rv 14.8mm. H, external view, lv, typical form, KL coll, Mediterranean Sea: height 79.6mm, width 65.8mm, depth of pv 40.0mm. I, L, KL coll, Bodrum, southern Aegean Sea. I, external view, lv. L, ventral view, pv. J, K, AMSC303118, 1 pv (juvenile), Filat, Israel. J, internal view, rv. K, external view, lv: height 29.5mm, width 31.5mm, depth of pv 14.1mm.





1 pv, same data as holotype; AMSC204279 1 pv, South side of Zaborgad Island, Red Sea, P. Clarkson, x 1994; AMSC99484, 1 pv (juvenile) Bay of Stari Grad, Bosnia, 2-10m, attached to rocks.

DESCRIPTION. Shell elongate-ovate to pear-shaped. Height to 80.7mm, approximately 1.74 times greater than the auricle width. Approximately equivalve, lv moderately convex; interior slightly excavated under hinge plate, with a strong, raised, coloured crenulated margin. Sculpture consists of numerous, strong, raised radial ribs; interstices narrow with a minor riblet centrally. Major ribs bear numerous spines varying from long and slightly spatulate to short or long and sharp. Lower (right) valve equally convex as the lv; ornamentation of unattached areas more densely spined than lv; cardinal area triangular; internally with a deep excavation under the hinge plate and a strong, coloured, raised crenulated margin. Fixation area large, with foliations supporting fixed area. Colour red-purple, lighter umbonally with indistinct black lines and markings at the umbonal region; internally blue-white with dark red-purple crenulated margin, external colour visible centrally. Based on 4 specimens.

TYPE LOCALITY. Ligurian Sea.

DISTRIBUTION AND HABITAT. Ligurian Sea - Red Sea; attached to corals or rock, to 25m.

REMARKS. *Spondylus cevikeri* sp. nov. most closely resembles *S. gaederopus* Linnaeus, 1758 in shape and colouration. *S. cevikeri* can be readily separated by the purple-coloured right valve (mostly white or orange in *gaederopus*), the numerous, equally sized radial ribs and smooth interstices (8-9 ribs ornamented with irregular shaped spines varying from spatulate to flat or sharp spines and interstices with dense small prickles in *gaederopus*), dark coloured lines and marks umbonally (absent in *gaederopus*) and purple internal crenulated margins in both valves (lv purple, rv usually white in *gaederopus*).

***Spondylus reevei* Fulton, 1915**

Spondylus hystrix Reeve, 1856: 12, 42, non Röding, 1798.

Spondylus reevei Fulton, 1915: 332, sp. 7.

Spondylus cuneus Lamprell 1986: pl. 8, figs 1A-D, non Reeve, 1856.

TYPE MATERIAL. HOLOTYPE: BMNH1984252/1, Philippine Islands.

DESCRIPTION. Shell elongately ovate, height to 90mm. Sculpture of many irregular ridges, ornamented with numerous, regular, strong, slightly depressed, blunt spines of varying lengths; interstices usually smooth but minor spines do occur in some specimens. Colour purple-red to brown, spines usually purple, internally white with a purple crenulated margin. Area of attachment variable.

DISTRIBUTION AND HABITAT. West Indies (Reeve, 1856), Mozambique, South Africa; and widely distributed throughout the Indo- and central Pacific; on and under dead coral, to 30m. Fine specimens have been collected from shipwrecks in the Solomon Islands and Palau.

REMARKS. This species was figured by Lamprell (1986) as a synonym of *S. cuneus* Reeve, 1856. Examination of numerous specimens of *S. americanus* Hermann, 1781 obtained by diving off Florida by Peter Clarkson, has, in our opinion, confirmed that *S. cuneus* is a junior synonym of that species.

***Spondylus limbatus* Sowerby, G.B. II, 1847**

Spondylus limbatus Sowerby, G.B. II, 1847: 427, fig. 51; Lamprell, 1986: pl. 16, fig. 2; Lamprell, 1998: pl. 2, figs 8, 10.

Spondylus radula Reeve, 1856: pl. 14, sp. 52;

Spondylus calcifer Carpenter, 1857: 152; Fulton, 1915: 357, sp. 68; Eisenberg, 1981: pl. 145, sp. 4; Lamprell, 1986: pl. 20, fig. 1; Skoglund & Mulliner, 1996: 102.

Spondylus smithi Fulton, 1915: 357, sp. 66.

TYPE MATERIAL. HOLOTYPE: BMNH 1846.12.4.1, Persian Gulf (sic).

DESCRIPTION. Shell ovate to elongately ovate, equivalve, height to 200mm. Sculpture of 6 principal radial ribs on top (lv) with spatulate appressed spines, stronger marginally, upright umbonally; interstices with numerous radial riblets with several stronger than the others and ornamented with similar but smaller spines than on the principal ribs; rv with numerous radial ribs

FIG. 2. A-D, *Spondylus* sp. 1 pv, FS coll, St Vincents, Cape Verde Islands. A, external view, lv. B, ventral view, pv. C, internal view, rv. D, internal view, lv: height 58.5mm, width 54.0mm, depth of pv 23.2mm. E, *Spondylus linguafelis* Sowerby, 1847, KL coll, Herald Prong Reef, Swain Reefs, external view, lv: height 41.5mm, width 39.0mm, depth of pv 19.7mm. F-K, *Spondylus cevikeri* sp. nov. F-J, holotype, AMS C204238, Ligurian Sea, 1 pv; F, external view, lv. G, external view, rv. H, ventral view, pv. I, internal view, rv. J, internal view, lv: height 80.7mm, width 76.5mm, depth of conjoined valves 43.1mm. K, paratype, AMSC99484, 1 pv (juvenile), Bosnia; external view, lv: height 27.3mm.



FIG. 3. A-C, *Spondylus cevikeri* sp. nov. A, paratype, AMSC204279, 1 pv, south side of Zaborgad Island, Red Sea, P. Clarkson, Oct 1994, external view, lv: height 49.1mm, width 40.7mm, depth of conjoined valves 29.1mm. B-C, paratype, QMMO66960, 1 pv, same data as holotype. B, external view, rv. C, internal view, lv. height 60.7mm, width 51.5mm, depth of conjoined valves 29.1mm. D-K, *Spondylus senegalensis* Schreibers, 1793. D, lectotype (illustration from Adanson, 1757). E-I, FS coll, Canary Islands. E, 1 pv, juvenile, external view, lv: height 24.2mm, width 26.0mm, depth of conjoined valves 13.3mm. F, 1 pv, juvenile, external view, lv: height 37.7mm, width 44.5mm, depth of conjoined valves 30.7mm. G, 1 pv, juvenile, external view, lv: height 41.0mm, width 47.0mm, depth of conjoined valves 27.8mm. H-I, 1 pv. H, internal view, rv; I, external view, lv: height 71.0mm, width 63.8mm, depth of conjoined valves 36.3mm. J-K, KL coll, 1 pv, Canary Islands. J, external view, lv. K, external view, rv: height 50.0mm, width 56.0mm, depth of conjoined valves 29.1mm.

and dense appressed, spatulate spines, interstices narrow with nine minor radial ribs and smaller, similar spines. Colour purple, maroon, orange, or brown with some yellow or white areas. Attachment area variable, but in larger specimens rv is usually entirely cemented to the substrate.

DISTRIBUTION AND HABITAT. Persian Gulf (Sowerby, 1847), Sea of Cortez, Mexico and Ecuador. Attached to coral rubble, dead shell debris, or solid rock, at 1–30m. Frequently covered with a greyish maroon sponge, which usually preserves the ornamentation of the shell.

REMARKS. Sowerby (1847) described *S. limbatus* from the Persian Gulf, however examination of numerous spondylids from that area has failed to identify *S. limbatus* among them. A comparison of *S. caleifer* Carpenter, 1857 collected in the Sea of Cortez (by Peter Clarkson) and the holotype of *S. limbatus* show these are the same. Hence, until there is evidence of *S. limbatus* from the Persian Gulf, this type locality should be regarded as erroneous.

***Spondylus* sp.**
(Fig. 2A–D)

MATERIAL. 1 pv, St Vincents, Cape Verde Islands, FS coll.

DESCRIPTION. Shell; ovate; height to 58.5mm, approximately 1.73 times greater than the auricle width; both valves moderately shallow. Sculpture of numerous fine radial ribs densely spined with short to long spatulate and sharp spines; interstices narrow with dense, short, minute spines. Colour of both valves purple, white at umbonal area; internally white, lv with purple crenulated inner margin, rv crenulated inner margin white, outer edge mauve. Area of attachment large.

DISTRIBUTION AND HABITAT. Cape Verde Islands; attached to coral, at 15–20m.

REMARKS. The equi-distant and close radial ribs, fine dense spines and purple right valve colouration distinguish the Cape Verde specimen from typical forms of *S. gaederopus*. *Spondylus* sp. is most similar to short spined *S. linguafelis* C.B. Sowerby II, 1847 from the Indo-Pacific and Australia and appears remarkably similar to a purple coloured, short spined form of this species from the Swain Reefs, Queensland (Fig. 2E). The locality, while previously considered very improbable for a predominantly Indo-Pacific species, is now acceptable in the light of known

ingress into the Mediterranean and Red Seas of other Indo-Pacific species of *Spondylus*. In the absence of additional material it is difficult to be certain of its correct identification.

***Spondylus senegalensis* Schreibers, 1793**
(Figs 3D–K, 4A–I)

Spondylus senegalensis Schreibers, 1793: 162; Lamprell 1986: pl. 17, fig. 3.

Spondylus powelli Smith, 1892: 36.

Spondylus horridus Dautzenberg, 1895 non Bellardi, 1852 (fossil).

MATERIAL. 3 pv, Puerto del Carmen, 1998, 20–30m by diver, FS coll; 7 pv, ix.1999, 20–30m, growth series, Los Canecijos, La Palma Island, FS coll; 1 pv, Lido, Funchal, Madeira, 20m by diver, FS coll; 1 pv, Sardina, FS coll, Canary Islands, KI coll.

DESCRIPTION. Shell pear- to fan-shaped; height to 150.0mm, approximately 1.88 times greater than the auricle width (based on measurements of 4 specimens). Approximately equivalve. LA with 4–11 principal radial ribs, ornamented with numerous short to moderately long, depressed, blunt and sharp spines; interstices with 5 or 6 minor radial ribs; minor ribs and interstices with dense, short overlapping minor spines or imbrications; rv sculpture where visible of strong, close, radial ribs with numerous overlapping spatulate to sharp spines. Specimens examined from Senegal usually have 4–5 radial ribs with strong overlapping spatulate spines, interstices devoid of spination. Colour orange red, bright red or brown with off-white spines, internally white with red or dark brown, wide crenulated margins in both valves.

TYPE LOCALITY. Senegal.

DISTRIBUTION AND HABITAT. Madeira, Porto Santo Island, Canary Islands, Cape Verde Islands, Senegal, Liberia, Ivory Coast, Principe Islands, Cameroons and Gabon; attached to rock or dead coral.

REMARKS. *Spondylus powelli* Smith, 1892 has been placed in the synonymy of *S. senegalensis* (Schreibers, 1793). However, until specimens including a growth series were recently obtained from Mr Frank Swinnen (Belgium), both species were considered valid by several authors. Mr Swinnen's specimens have enabled a thorough examination and comparison of numerous variable forms of the species which show that although the typical fan-shaped Senegal specimens differ from the larger and often pear-shaped specimens from other localities, there is insufficient variation to separate the two

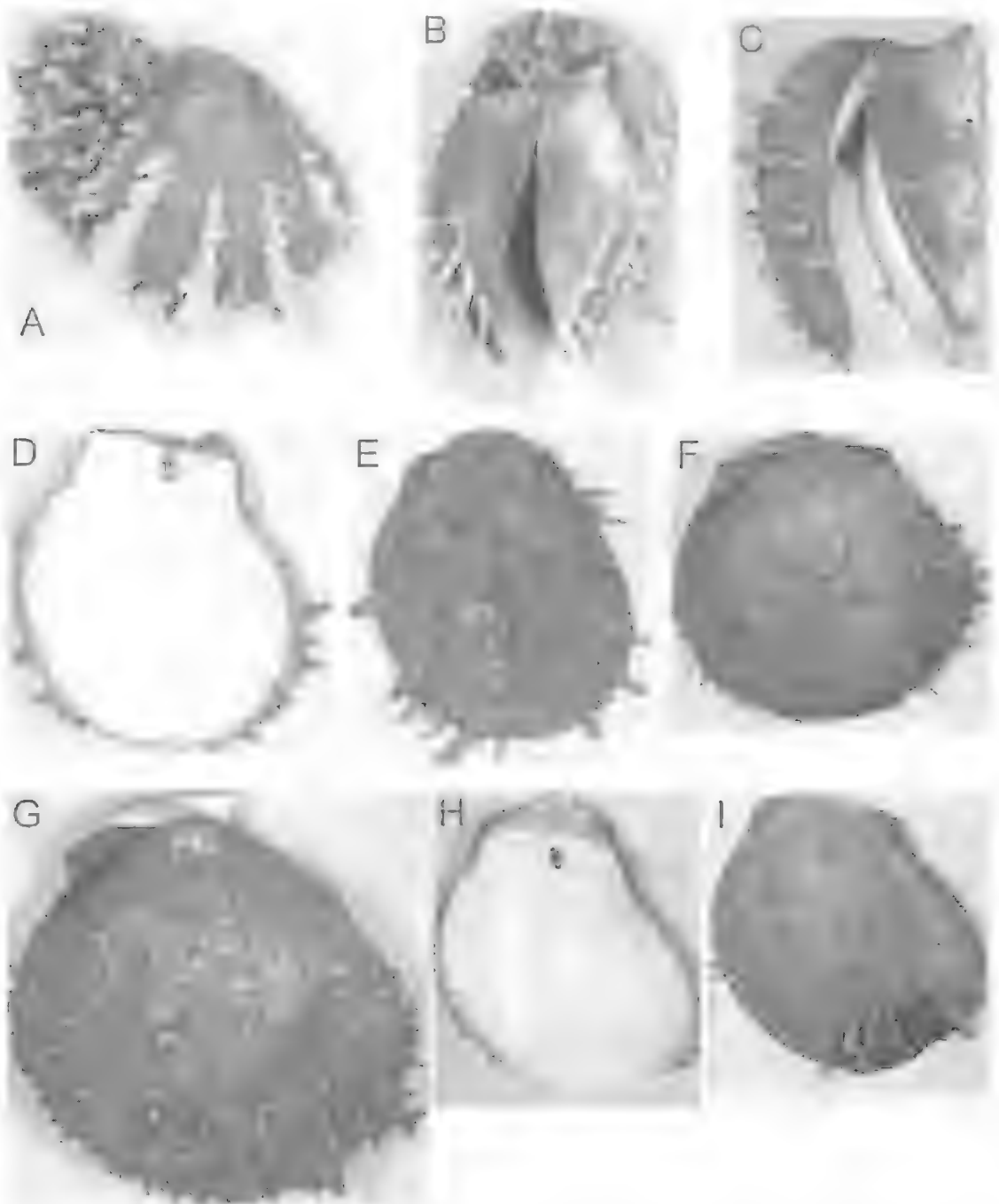


FIG. 4. *Spondylus senegalensis* Schreibers, 1793, Guinea, FS coll. A-B, 1 pv. A, external view, lv. B, dorsal view, pv; height 59.5mm, width 57.5mm, depth of conjoined valves 40.6mm. C, F, 1 pv; C, dorsal view, pv. F, external view, lv; height 89.0mm, width 83.2mm, depth of conjoined valves 50.2mm. D-E, 1 pv. D, internal view rv. E, external view of lv; height 118.7mm, width 98.3mm, depth of conjoined valves 59.5mm. G, 1 pv, external view of lv; height 115.8mm; width 119.7mm; depth of pv 71.2mm. H-I, 1 pv. H, internal view of rv. I, external view, lv; height 84.5mm; width 81.9mm; depth of pv 42.0mm.

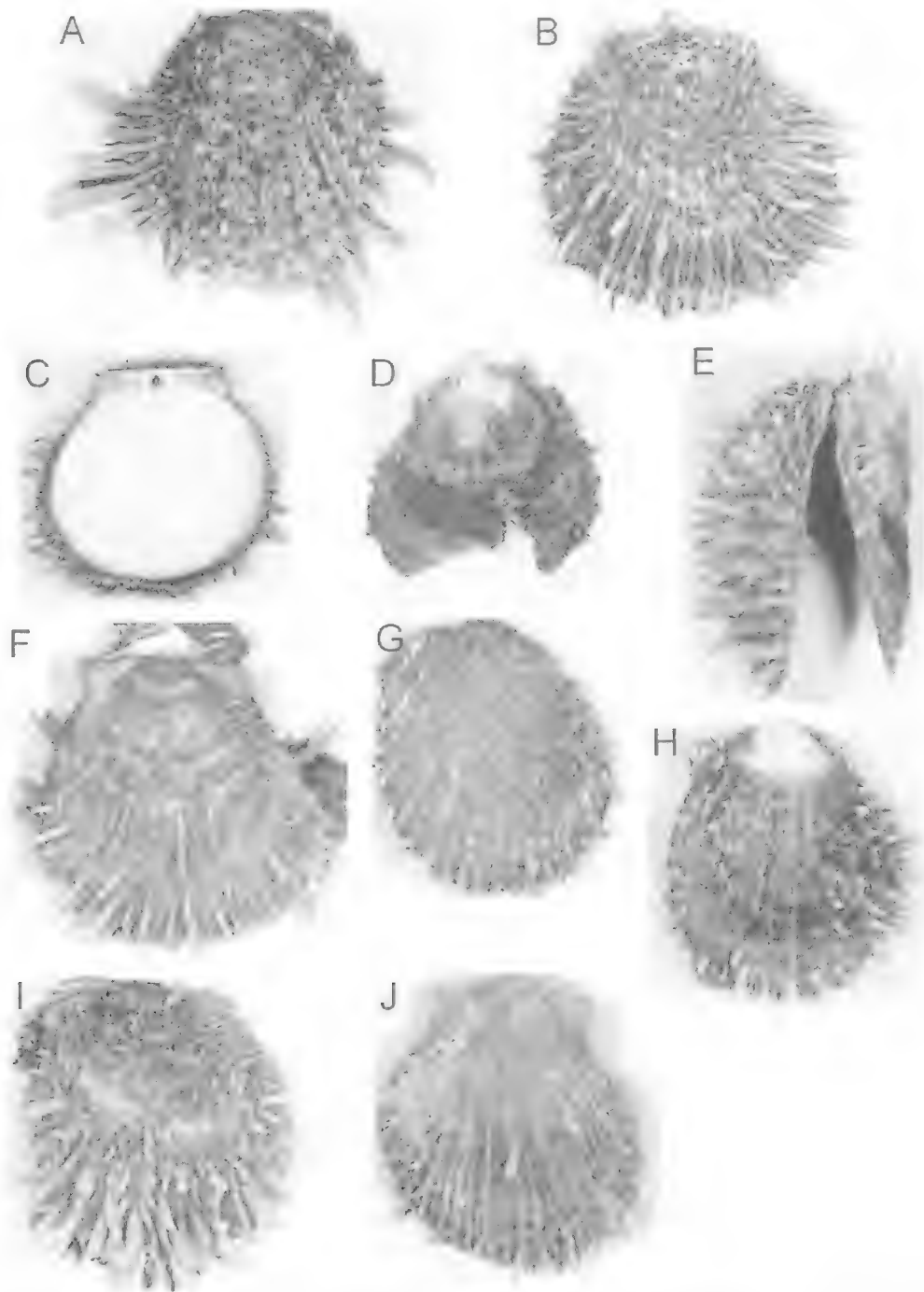


FIG. 5. *Spondylus multisetosus* Reeve, 1856. A, BMNH1998094, syntype, external view, lv. B-E, Mediterranean Sea, DC coll No. 281. B, external view, lv. C, internal view, lv. D, external view, rv. E, dorsal view, pv: height 70.2mm, width 75.2mm, depth of conjoined valves 36.6mm. F, Cebu I., Philippine Islands, KL coll, external view of lv: height 59.8mm, width 52.2mm, depth of conjoined valves 31.0mm. G-I, Mediterranean Sea, DC coll, G, No. 269, external view, lv: height 72.5mm, width 67.9mm, depth of conjoined valves 44.3mm. H, No. 270, external view, lv: height 85.0mm, width 77.0mm, depth of conjoined valves 47.5mm. I, No. 233, external view, lv: height 73.0mm, width 65.5mm, depth of conjoined valves 43.3mm. J, Capricorn Channel, Qld, 127m, KL coll, external view of lv: height 71.8mm, width 64.6mm, depth of conjoined valves 40.2mm.

forms. As a growth series of this unusual species has not been previously figured, a plate showing shape, size and sculpture variations is included.

***Spondylus multisetosus* Reeve, 1856**
(Fig. 5A-J)

Spondylus multisetosus Reeve, 1856: pl. 3, fig. 11; Fulton, 1915: 353, sp. 48; Lamprell, 1986: pl. 13, fig. 1.

MATERIAL. 4 specimens, DC coll.; nos 233, 270, Tasucu, Turkey; nos 269, 281, Iskenderun, Turkey.

DESCRIPTION. Shell ovate, height to 68mm; approximately 2.48 times greater than the auricle width (based on measurements of 4 specimens). Lv usually more inflated than the rv. Sculpture of numerous radial ribs and striae with numerous upright spines, hollowed underneath with some remote, slightly spatulate spines; interstices densely ribbed, ornamented with small sharp spines. Colour mauve or brown with some yellow on ribs and spines, sometimes yellow white, dark coloured umbonally; internally blue white with a moderately wide, dark purple-brown or variegated yellow and brown crenulated margin.

TYPE LOCALITY. Philippine Islands.

DISTRIBUTION AND HABITAT. Indo-Pacific (Philippines); Mediterranean Sea; attached to Hammer Oysters, shell debris, corals or rock in shallow, turbid water.

REMARKS. These specimens confirm this Indo-Pacific species in the Mediterranean Sea. The brown or mauve base colour and yellow upright spines distinguish *S. multisetosus* from any other Mediterranean species.

***Spondylus spinosus* Schreibers, 1793**
(Fig. 6A-J)

Spondylus spinosus Schreibers, 1793: 154 (based on Chemnitz, 1784: fig. 460); Oyama & Takemura, 1960: 97, fig. 2; Habe 1977: 93; Lamprell, 1986: pl. 14, fig. 2a-b; Mienis et al., 1993.

Spondylus proboscideus Schreibers, 1793: 468, pl. 145, sp. 11.

Spondylus aculeatus Schreibers, 1793: 476.

Spondylus marisrubri Röding, 1798: 460.

Spondylus dentatus Chenu, 1845: pls 25, 27.

Spondylus lamarecki Chenu, 1845: pl. 9, figs 3-4; Lamprell, 1986: pl. 15, fig. 3.

Spondylus aculeatus Sowerby, 1847: figs 11-13.

TYPE LOCALITY. Red Sea.

DISTRIBUTION AND HABITAT. Mediterranean Sea, Red Sea, Indo-Pacific (Japan, Philippines, Mauritius, Solomon Islands, north Western Australia); attached to dead coral or debris in 3m or more of water. A species frequently found within protected lagoonal environments, where it grows amongst delicate *Acropora* corals.

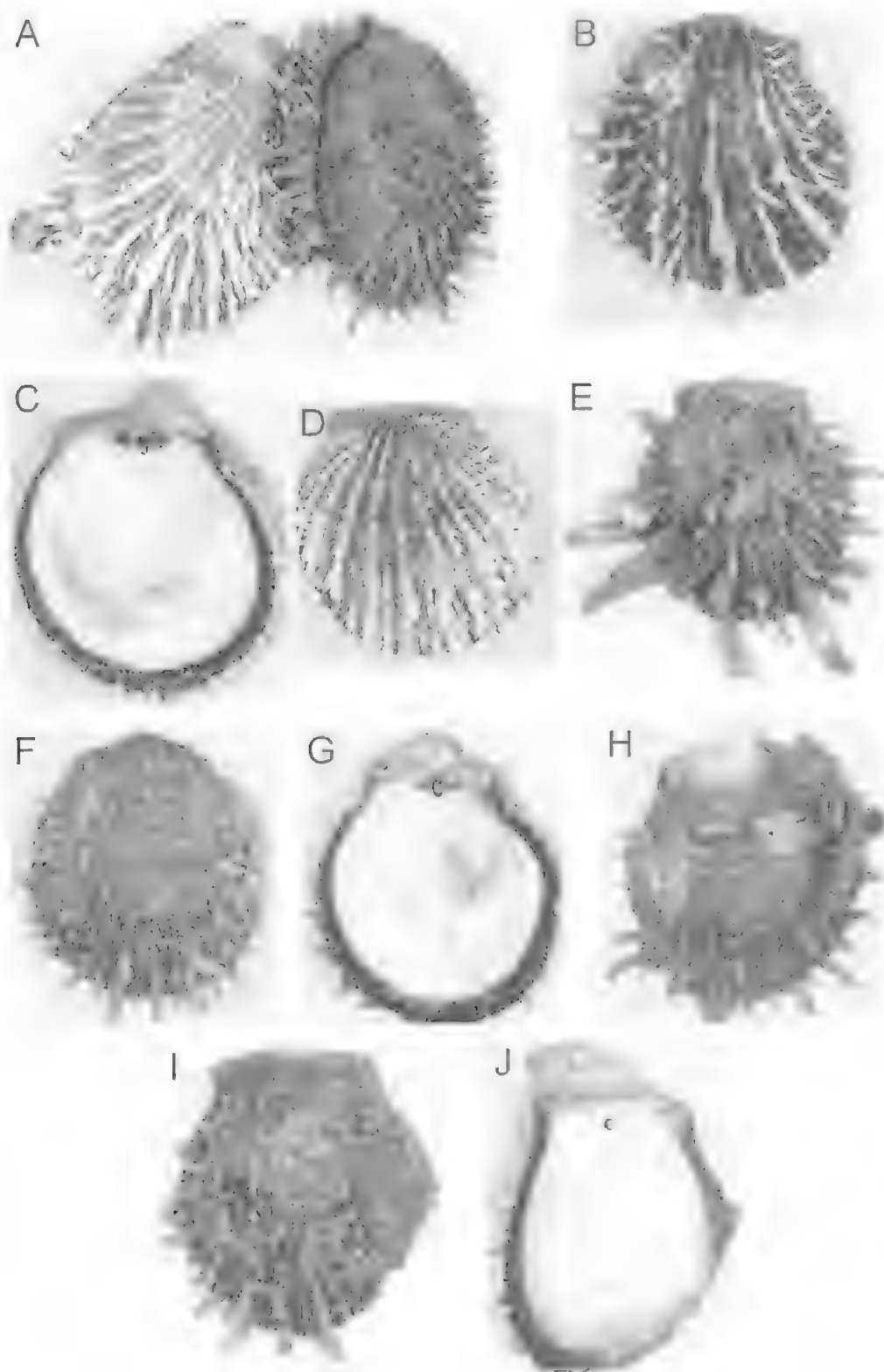
REMARKS. Some authors have considered *Spondylus lamarecki* Chenu, 1845 to be a variety of *S. squamosus* auct., non Schreibers, 1793 (= *S. sinensis* Schreibers, 1793) however, in *S. lamarecki* the interstitial areas are quite narrow and the shell more elongate. After examining numerous specimens we consider *S. lamarecki* to be a form of *S. spinosus* Schreibers. We have figured a wide variety of the species from the typical form with dark coloured base, white ribs and spines to the all-brown and long spined forms. Small specimens can bear long spines, but these erode as the shell grows, leaving the shell rather poorly sculptured in its adult state.

ACKNOWLEDGEMENTS

We would like to thank the following museum staff and collectors for their assistance;

Ms Kathie Way and Mrs Joan Pickering of the Malacology Section of The Natural History Museum, London for the loan of specimens and supplying information on the status of specimens in the collection; Dr Philippe Bouchet, Muséum National d'Histoire Naturelle, Paris for the loan of type material; Dr Claude Vaucher and Dr Yves Finet, Muséum d'Histoire Naturelle, Geneva; Dr John Healy, University of Queensland, Brisbane for helpful advice on the presentation of this paper; Mr Ian Loch, Malacology Section, Australian Museum, Sydney for the loan of specimens; Dr Michele Dardano, Mr Frank Swinnen, and Mr Dogan Ceviker donated material. Thanks are also due to Darryl Potter, Malacology Section, Queensland Museum for his helpful comments on the manuscript. The Malacological Society of Australasia provided tavel assistance.

FIG. 6. *Spondylus spinosus* Schreibers, 1793. A, Mediterranean Sea (off coast of Turkey), DC coll nos 239-240, external view of two joined pvs, one all brown, one (largest) typically brown with white ribs and spines: height 89.5mm, width 76.5mm, depth of conjoined valves 56.4mm. B, external view of a lv: height 58.0mm, width 53.4mm, depth of lv 19.6mm. C-D, 1 pv; C, internal view, rv. D, external view, lv: height 78.2mm, width 73.9mm, depth of conjoined valves 45.8mm. E, external view of a lv: height 53.1mm, width 47.3mm. F-G, 1 pv, No. 246. F, external view, lv; G, internal view, rv: height 92.6mm, width 91.6mm, depth of conjoined valves 47.0mm. H, external view of a rv: height 68.0mm, width 64.5mm, depth of rv 20.0mm. I-J, 1 pv; I, external view, lv. J, internal view of rv: height 62.2mm, width 53.5mm, depth of conjoined valves 35.3mm.



LITERATURE CITED

- ABBOTT, R.T. & DANCE, S.P. 1982. Compendium of seashells. (E.P. Dutton: New York).
- ADANSON, M. 1759. Histoire naturelle du Sénégal. Coquillages avec la relation abrégée du voyage fait en ce pays, etc. Illust. (London).
- CHEMNITZ, J.H. 1784. Neues systematisches conchylien-cabinet. Vol 7. G.N. (Raspe: Nürnberg).
- DODGE, H. 1952. A historical review of the mollusks of Linnaeus. Bulletin of the American Museum of Natural History 100: 242-260.
- FULTON, H.C. 1915. List of the Recent species of *Spondylus* Linne with some notes and descriptions of six new forms. Journal of Conchology 14: 331-360.
- LAMPRELL, K.L. 1986. *Spondylus*, spiny oysters of the world. (E.J. Brill-Dr W. Backhuys: Leiden).
- 1992a. Notes on *Spondylus* Linnaeus with descriptions of two new species from Western Australia (Mollusca: Bivalvia: Spondylidae). Memoirs of the Queensland Museum 32: 189-194.
- 1992b. On some species of *Spondylus*. La Conchiglia 23: 40-41.
1998. Recent *Spondylus* from the Middle East and adjacent regions, with the description of two new species (Mollusca, Bivalvia, Pectinoidea). Vita Marina 45: 41-60.
- LINNAEUS, C. 1758. Systema Naturae, per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. 10th edition. (Holmiae: Laurentii Salvii).
- LUCAS, M. 1978. Pectinoidea from the European coasts. La Conchiglia 116-7: 6-8.
- MIENIS, H.K., GALILI, E. & RAPOPORT, J. 1993. The Spiny Oyster, *Spondylus spinosus*, a well-established Indo-Pacific bivalve in the Eastern Mediterranean off Israel (Mollusca, Bivalvia, Spondylidae). Zoology in the Middle East 9: 83-91.
- MONTEROSATO, T.A. di 1875. Nuova rivista delle conchiglie Mediterranee. Atti della Accademia Palermitana scienze e lettere. new series, 5: 1-50.
- PALLARY, P. 1904. Coquilles marines du littoral du département D'Oran. Memoires du Muséum national d'Histoire Naturelle de Paris. Journal de Conchyliologie. 48: 211-434.
- REEVE, L.A. 1856. Monograph of the genus *Spondylus*. Conchologia Iconica or illustrations of the shells of molluscous animals, Vol. 9. (Reeve: London).
- RÖDING, P.F. 1798. Museum Boltenianum sive Catalogus cimeliorum e tribus regnis naturae. Pars secunda, Conchylia sive Testacea univalvia, bivalvia & multivalvia. (J.C. Trappii: Hamburg).
- SCHREIBERS, K. 1793. Versuch einer Vollständigen Conchylienkenntniss nach Linné's System. (Vienna).
- SMITH, E.A. 1892. Description of a new species of *Spondylus* and a new *Helix*. Journal of Conchology 7: 71.
- SOWERBY, G.B. II 1847. Descriptions of several new species of *Spondylus*. Proceedings of the Zoological Society of London 1847: 86-88.
- SPRINGSTEEN, F.J. & LEOBRERA, F.M. 1986. Shells of the Philippines. (Carfel Seashell Museum: Manila).

SOME SPONDYLIDS FROM THE PACIFIC OCEAN (MOLLUSCA: BIVALVIA: SPONDYLIDAE)

KEVIN LAMPRELL, JOHN STANISIC AND PETER CLARKSON

Lamprell, K., Stanisic, J. & Clarkson, P. 2001 06 30: Some spondylids from the Pacific Ocean (Mollusca: Bivalvia: Spondylidae). *Memoirs of the Queensland Museum* **46**(2): 623-628. Brisbane. ISSN 0079-8835.

Spondylus swinneni sp. nov. is described and figured; the type of *Spondylus multimuricatus* Reeve, 1856 is figured and redescribed; *Spondylus hawaiiensis* Dall, Bartsch & Rehder, 1938 is placed in the synonymy of *Spondylus candidus* Lamarck, 1819; *Spondylus puniceus* Bernard, Cai & Morton, 1993 (nom. nov. for *Spondylus coccineus* Lamarck, 1819 non Schreibers, 1793) is discussed. □ *Spondylus*, new species, Pacific Ocean.

Kevin Lamprell & John Stanisic, Queensland Museum, PO Box 3300, South Brisbane 4101, Peter Clarkson, PO Box 713, Port Lincoln 5606; 8 May 2000.

Since publication of 'Spondylus, Spiny Oyster Shells of the World' (Lamprell, 1986), several important taxonomic changes have been effected within the Spondylidae (Lamprell, 1992a; Lamprell, 1992b; Lamprell & Kilburn, 1995; Skoglund & Mulliner, 1996; Lamprell, 1998; Lamprell & Dekker, in press; Lamprell & Willan, 2000; Lamprell & Healy, 2001). Thirteen new species have been described and several species listed in the book have been placed in synonymy. These changes were largely based on the results of extensive deep-water exploration off the coast of New Caledonia by the ORSTOM expeditions (Lamprell & Healy, 2001) and diving off the American coast and Solomon Islands. As a result there has been renewed interest shown in the group by collectors in Europe, Australia and other Indo-Pacific countries and consequently much more material from private collections has become available for scrutiny. The present study aims to rectify several additional taxonomic problems that have come to notice following examination of this material.

ABBREVIATIONS. QM, Queensland Museum, Brisbane; AMS, Australian Museum, Sydney; BMNH, The Museum of Natural History, London; MNHN, Muséum National d'Histoire Naturelle, Paris; MHNG, Muséum d'Histoire Naturelle, Geneva; USNM, United States National Museum, Washington; KL coll, Kevin Lamprell collection; PC coll, Peter Clarkson collection; lv, left valve; rv, right valve; pv, paired valve; NSW, New South Wales; WA, Western Australia; Qld, Queensland.

MEASUREMENT DETAILS. Height = greatest vertical distance between the centre of the umbo and the lowest part of the ventral margin of lv,

excluding spines. Width = greatest horizontal distance between the anterior and dorsal margins of lv, excluding spines. Depth of pv = greatest distance between the external surfaces of the left and right valves excluding the ribs and spines.

Family SPONDYLIDAE Gray, 1826

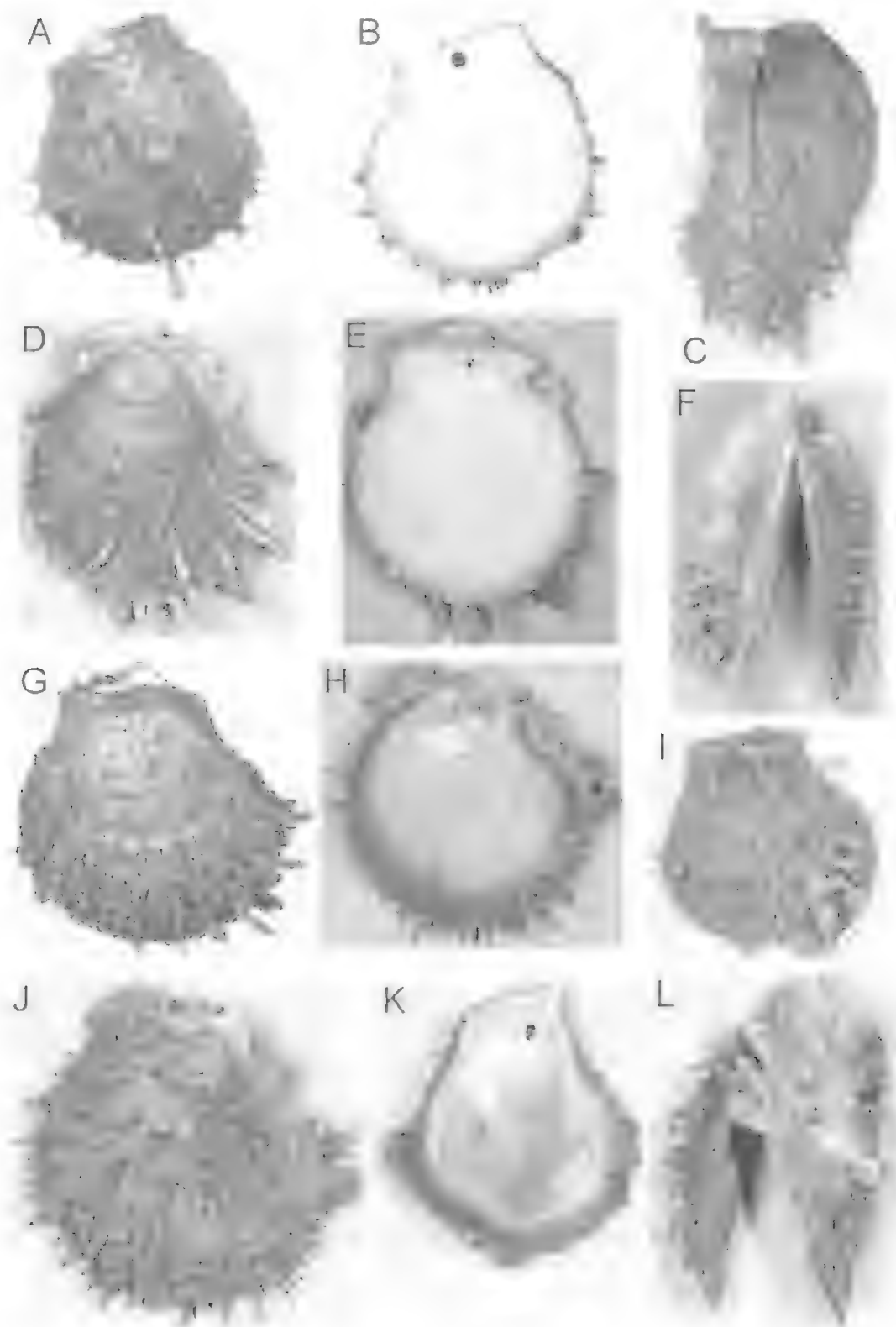
***Spondylus swinneni* sp. nov.**
(Fig. 1G-K)

Spondylus multimuricatus Reeve, 1856: Lamprell, 1986: 32; pl. 9, fig. 2a-b, non Reeve, 1856.

ETYMOLOGY. For Mr Frank Swinnen.

TYPE MATERIAL. HOLOTYPE: AMSC303105, Philippine Islands. PARATYPES: AMSC303116, northern Qld; QMMO66961, Finger Reef, Swains Reef Qld, off corals, 18m, P. Clarkson. OTHER MATERIAL. KL coll, 1 pv, Bonegi Wreck, Solomon Islands, 28.viii.85; KL coll, 1 pv, West of Honiara, Solomon Islands, dived, P. Clarkson; KL coll, 2pv, Gneering Shoals, south Qld, dived 6-30m, P. Clarkson; PC coll, 9pv, West of Honiara, Solomons, dived 7-50m, shipwrecks and reefs, P. Clarkson; PC coll, 1 pv, Santo, Vanuatu, 8m; PC coll, 1 pv, North West Reef, Exmouth, WA, 24m, P. Clarkson.

DESCRIPTION. Shell elongate-ovate to ovate, height to 125mm; lv moderately convex to flat, width of the auricles approximately half the height of the shell. Sculpture consisting of numerous radial ribs; interstices wider than the ribs with one or two minor riblets. Major ribs bearing numerous overlapping spines varying from short to moderately long, sharp, blunted or slightly spatulate, frequently curved inward and hook-like. Internally slightly excavated under the hinge; pearl white centrally, deep brown outer crenulated margin, orange to yellow-brown at the crenulations and lighter brown inner margin. Rv slightly more convex than the lv; ornamentation



of unattached areas consisting of evenly spaced radial ribs and dense overlapping spines, sharp and hook-like, rarely if ever blunt or spatulate. Cardinal area triangular; internally with a shallow excavation under the hinge plate and a strong, crenulated margin similarly coloured to the lv. Area of attachment variable with limited foliations supporting fixed area. Colour orange-brown with indistinct black lines and markings at the umbonal region; some specimens have black in the interstitial areas extending to the lower margin.

TYPE LOCALITY. Philippine Islands.

DISTRIBUTION AND HABITAT. Indo-Pacific, Solomon Islands, and northern Australia; cemented to ledges, overhangs, and cave walls, frequently along drop-offs festooned with gorgonian corals and subject to moderate currents, in 10 to more than 50m. Delicately sculptured specimens have been collected from sheltered positions within shipwrecks at similar depths.

REMARKS. Specimens of *Spondylus swinneni* sp. nov. have been confused with *S. multimuricatus* Reeve, 1856 in the past (Lamprell, 1986). However, compared with the latter species the hinge teeth of *S. swinneni* are finer and tinged with brown, the spines overlap and are not arranged concentrically, the ribs are more numerous and less prominent. The ornamentation of the lv of *S. swinneni* is of short to moderate length spines, deposited evenly on the ribs, and consistently sharp and hook-like (on the lv of *S. multimuricatus* the major spines are relatively broad and blunt while the species has a limited number of prominent ribs). *Spondylus swinneni* is also superficially similar to the sympatric *S. linguafelis* Sowerby, G. B. II, 1847. However, the shorter, spatulate or hook-like spines (longer and needle-like in *S. linguafelis*) readily distinguishes the new species.

***Spondylus multimuricatus* Reeve, 1856**
(Fig. 1A-F)

Spondylus multimuricatus Reeve, 1856: pl. 4, fig. 15; Fulton, 1915: 353, sp. 49; Abbott & Dance, 1986 (3rd ed.): 316.

TYPE MATERIAL. Specimen figured by Reeve, BMNH1998093/1 lectotype herein selected, Philippine Islands; paralectotype, BMNH1998093/2, same data as lectotype. Dimensions of lectotype: height 70.5mm, width 64.0mm, depth of pv 35.0mm. OTHER MATERIAL. KL coll, 1 pv, Koh Samui, southeast Thailand, Gulf of Siam; KL coll, 1 pv, Cebu Islands, Philippines, by dealer; KL coll, 1 pv, Heron Island, Qld, L. Newman; KL coll, 1 pv, Exmouth Gulf, north W.A, P. Clarkson.

DESCRIPTION. Shell elongate-ovate, moderately gibbous, height to 100mm. Sculpture of numerous weakly formed ribs, 5-6 of which are ornamented with irregular squamate, short to long spines; interstices with numerous minor radial ribs that are densely spined with minor spines; 2-3 interstitial ribs bear slightly larger sharp spines of varying lengths. Colour red-orange, orange or mauve with some purple at the umbonal area; internally white; crenulated margins deep-orange. Area of attachment variable.

TYPE LOCALITY. Philippine Islands.

DISTRIBUTION AND HABITAT. Philippine Islands; habitat unknown.

REMARKS. *Spondylus multimuricatus* was incorrectly figured by Lamprell (1986) and Springsteen & Leobrera (1986). The species figured by Lamprell, 1986 is *S. swinneni* sp. nov. (see above). The species figured by Springsteen & Leobrera (1986) is a specimen of *S. reesianus* Sowerby, 1903.

***Spondylus candidus* Lamarck, 1819**
(Fig. 2A-H)

Spondylus candidus Lamarck, 1819: 188.

Spondylus candidus Lamarck: Chenu, 1845: pl. 12, fig. 4; Sowerby II, 1848: figs 3-5; Reeve, 1856: sp. 2; Fulton, 1915: 358, sp. 74; Springsteen & Leobrera, 1986: pl. 92, fig. 6; Lamprell, 1986: pl. 25, fig. 3a-b; Lamprell & Kilburn, 1995: 91, figs d-e (as *flabellum*); Lamprell, 1998: pl. 3, figs 9-11.

Spondylus hawaiiensis Dall, Bartsch & Rehder, 1938: 100.

TYPE MATERIAL. HOLOTYPE: MNHN, Lamarck Collection. (Lamprell, 1986: pl. 3, fig 9); Holotype of *Spondylus hawaiiensis*, USNM337515. OTHER MATERIAL. KL coll, 1 pv, Koko Crater, Hawaii, attached under boulder at 22m, 1996, Chris Takahashi; KL coll, 1

FIG. 1. A-F. *Spondylus multimuricatus* Reeve, 1856. A-C, lectotype herein selected, BMNH1998093/1, Philippine Islands. A, external view lv. B, internal view rv. C, ventral view pv; height 69.3mm, width 63mm, depth of pv 36.3mm. D-F, paralectotype herein selected BMNH1998093/2, Philippine Islands. D, external view lv. E, internal view rv. F, ventral view pv; height 74.0mm, width 66.0mm, depth of pv 48.0mm. G-L, *Spondylus swinneni* sp. nov. G, holotype, AMSC303105, Philippine Islands, external view lv. H-J, KL coll, 1 pv, Bonegi Wreck, Solomon Islands. H, internal view rv. I, ventral view pv. J, external view lv; height 27.0mm. K-L, paratype, QMMO66961, 1 pv, off corals, Finger Reef, Swains Reef, Qld, 18m. K, internal view rv. L, external view lv.

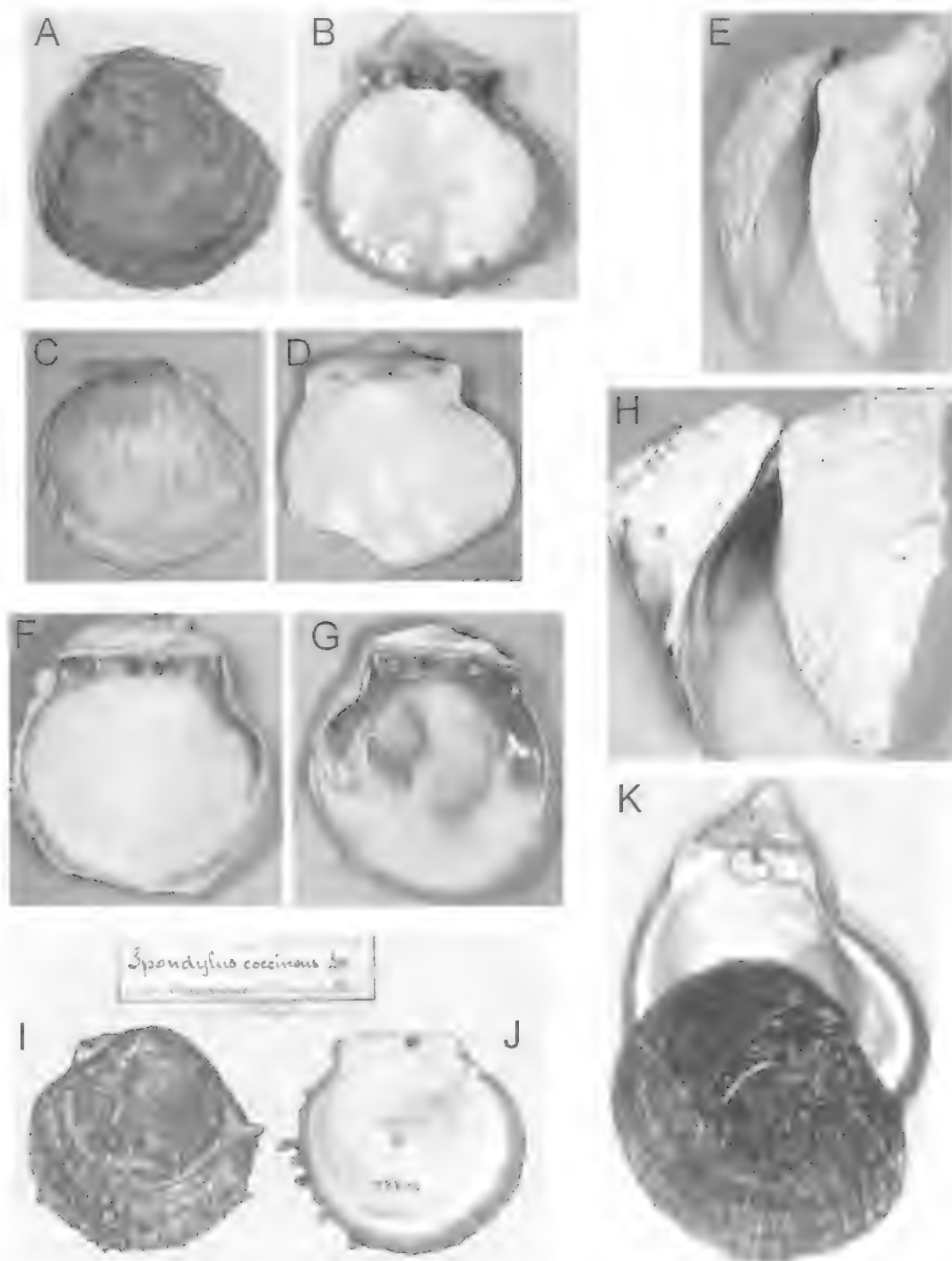


FIG. 2. A-H, *Spondylus candidus* Lamarck, 1819. A,B, KL coll, 1 pv, SW side Cassin I., N of Broome, WA, 13m. A, external view lv. B, internal view rv. C-E, KL coll, 1 pv, Koko Crater, Hawaii, 17m. C, external view lv. D, internal view rv. E, ventral view pv. F-H, KL coll, 1 pv, Oahu, attached under ledge on ceiling, 18m. F, internal view lv. G, internal view rv. H, ventral view pv. I,J, 1 pv, MHNG1088/96, specimen labelled '*Spondylus coccineus* Lk Type locality Amérique? Chenu 15/3 No 11'. I, external view lv. J, internal view rv. K, 1 pv, MNHN, specimen labelled '*Spondylus coccineus* Lam nomme par Lamarck', external view lv and view of hinge of rv.

pv, Oahu, attached under ledge on ceiling, 20m, 1999, Chris Takahashi; KL coll, 1 pv + attached pv juvenile, Hakeiwa, Oahu, attached under ledge at c.20m, 1999, Chris Takahashi; KL coll, 1 pv, inside lagoon, Pt Havau, Moorea, Tahiti; KL coll, 1 pv, SW side Cassini I., N of Broome, 13m, WA, P. Clarkson.

TYPE LOCALITY. Nouvelle-Hollande [= Australia].

DISTRIBUTION AND HABITAT. Mozambique-South Africa, Japan (as *S. flabellum*) and Indo-West Pacific, Hawaii, Qld, north WA; common under dead coral slabs or on the under faces of huge living *Porites* coral colonies also occurs in marine caves or on the walls of shipwrecks in 1-40m.

REMARKS. While we have been unable to obtain the holotype of *Spondylus hawaiiensis*, Kay (1979) synonymised it with *S. tenebrosus* Reeve, 1856 (= *S. violaceus* Reeve, 1856). Specimens of *S. hawaiiensis* sent by Mr Chris Takahashi for examination, after cleaning, proved to be inseparable from *S. candidus*. Further examination of specimens of *S. hawaiiensis* in the collection of one of the authors (KL) has led us to conclude that these two species are the same.

Spondylus punicus Bernard, Cai & Morton, 1993 (Fig. 2I-K)

Spondylus punicus Bernard, Cai & Morton, 1993: 55 (nom. nov. for *Spondylus coccineus* Lamarck, 1819, non Schreibers, 1793).

Spondylus coccineus Lamarck, 1819: 190, non Schreibers, 1793.

Spondylus coccineus Lamarck: Chenu, 1845: pls 14, 15 (not pl. 25, fig. 2); Reeve, 1856: sp. 44; Fulton, 1915: 336, sp. 31; Lamprell, 1986: 70, fig. 1.

Spondylus coccineus var. *vaillanti* Jousseaume (in Lamy), 1927: 301.

DISTRIBUTION AND HABITAT. Indian Ocean, Philippines, South and east China to Okinawa (Bernard, Cai & Morton, 1993); attached to corals in moderately deep water.

REMARKS. *Spondylus coccineus* Lamarck (non Schreibers, 1793) was briefly described by Lamarck (188: 11) without a stated locality. Examination of the Lamarck specimen marked '*Spondylus coccineus* (pl. 2, fig. 11)' in the MNHN showed a pear-shaped spondylid with narrow, oblique auricles and dense radial ribs devoid of ornamentation, probably due to age and deterioration; internally off-white with a raised crenulate, dark coloured margin. A specimen marked '*Spondylus coccineus* Lk Type' (pl. 2, fig. 9-10) with the locality 'Amérique?' Chenu

15/3 No 11, registration number 1088/96 is in the collections of the MHNG. This specimen is ovate, with wide interstices and strong, sparse spines on the 5 or 6 principal ribs. The specimen is tan-brown in colour with a light orange coloured internal crenulated margin. The specimen bears a strong resemblance to *S. gilvus* Reeve, 1856. In our opinion both *S. coccineus* type specimens are of doubtful status. Bernard, Cai & Morton (1993) introduced the replacement name *S. punicus* for this species. They recorded the species as occurring in China but gave no reference to the specimen(s) on which they based their identification.

ACKNOWLEDGEMENTS

We would like to thank the following, museum staff and collectors for their assistance. Ms Kathie Way, malacology section of The Natural History Museum, London for the loan of specimens and access to the type collection; Dr Philippe Bouchet, Muséum National d'Histoire Naturelle, Paris for permission to access the type collection and loan of type material; Dr Claude Vaucher and Dr Yves Finet, Muséum d'Histoire Naturelle, Geneva for access to the type collection; Mr Ian Loch, Malacology Section of the Australian Museum, Sydney for the loan of specimens. Mr Chris Takahashi, Hawaii donated Hawaiian *Spondylus* specimens. The Malacological Society of Australasia provided travel assistance to KL.

LITERATURE CITED

- ABBOTT, R.T. & DANCE, S.P. 1982. Compendium of seashells. (E.P. Dutton: New York).
- BERNARD, F.R., CAI, Y. & MORTON, B. 1993. Catalogue of the living marine bivalve molluscs of China. (Hong Kong University Press: Hong Kong).
- CHEMNITZ, J.H. 1784. Neues systematisches conchylien-cabinet. Vol 7. (G.N. Raspe: Nürnberg).
- CHENU, J.C. 1845. Illustrations conchyliologiques Vol. 3. Bivalves. Part 2.
- DALL, W.H., BARTSCH, P. & REHDER, H.A. 1938. A manual of the Recent and fossil marine pelecypod mollusks of the Hawaiian Islands. Bulletin of the Bishop Museum 153: 1-233.
- FULTON, H.C. 1915. List of the Recent species of *Spondylus* Linné with some notes and descriptions of six new forms. Journal of Conchology 14: 331-360.
- KAY, E.A. 1979. Hawaiian marine shells. Reef and shore fauna of Hawaii. Section 4. Mollusca. B.P. Bishop Museum Special Publication 64 (4): 1-653.

- LAMPRELL, K.L. 1986. *Spondylus*, spiny oysters of the world. (E.J. Brill-Dr W. Backhuys: Leiden).
- 1992a. Notes on *Spondylus* Linnaeus with descriptions of two new species from Western Australia (Mollusca: Bivalvia: Spondylidae). *Memoirs of the Queensland Museum* 32: 189-194.
- 1992b. On some species of *Spondylus*. *La Conchiglia* 23: 40-41.
- LAMPRELL, K.L. & DEKKER, H. In press. Rectification of nomenclature and notes on species of *Spondylus* Linnaeus, from the Chemnitz Cabinet and held in the Zoological Museum, University of Copenhagen (Mollusca: Bivalvia: Pectinoidea: Spondylidae).
- LAMPRELL, K.L. & KILBURN, R.N. 1995. The recent Spondylidae of South Africa and Mozambique, with the description of a new species (Mollusca, Bivalvia, Pectinoidea). *Molluscan Research* 16: 81-95.
- LAMPRELL, K.L. & WILLAN, R.C. 2000. Rectification of nomenclature for three species of *Spondylus* Linnaeus (Bivalvia: Pectinoidea: Spondylidae) from the Indo-Pacific based on re-examination of type specimens. *Vita Marina* 47: 1-7.
- LAMPRELL, K.L. & HEALY, J.M. 2001. The Recent Spondylidae from New Caledonian and adjacent waters, with the descriptions of 8 new species, and some taxonomic notes on the species *Spondylus anacanthus* (Mawe) (Mollusca, Bivalvia, Spondylidae). *Bulletin du Muséum National d'Histoire Naturelle. Paris (Zoologie)* 22.
- LAMY, E. 1927. Les Spondyles de la Mer Rouge (d'après les matériaux recueillis par le Dr Jousseume). *Bulletin du Muséum National d'Histoire Naturelle* 33: 259-266; 301-308.
- LINNAEUS, C. 1758. *Systema Naturae*, per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. 10th edition. (Holmiae: Laurentii Salvii).
- REEVE, L.A. 1856. Monograph of the genus *Spondylus*. *Conchologia Iconica* or illustrations of the shells of molluscos animals, Vol. 9. (Reeve: London).
- SCHREIBERS, K. 1793. Versuch einer Vollständigen Conchylienkenntniss nach Linné's System. (Vienna).
- SKOGLUND, C. & MULLINER, D.K. 1996. The genus *Spondylus* (Bivalvia: Spondylidae) of the Panamic Province. *The Festivus* 28: 93-107.
- SOWERBY, G.B. II 1847. Descriptions of several new species of *Spondylus*. *Proceedings of the Zoological Society of London* 1847: 86-88.
- SPRINGSTEEN, F.J. & LEOBRERA, F.M. 1986. *Shells of the Philippines*. (Carfel Seashell Museum: Manila).

A BREEDING POPULATION OF THE YELLOW-BELLIED SEA SNAKE, *PELAMIS PLATURUS*, IN THE GULF OF CARPENTARIA

COLIN J. LIMPUS

Limpus, C.J. 2001 06 30: A breeding population of the Yellow-bellied sea-snake, *Pelamis platurus*, in the Gulf of Carpentaria. *Memoirs of the Queensland Museum* 46(2): 629-630. Brisbane. ISSN0079-8835.

A surface aggregation of *Pelamis platurus* was observed on 13 July 1992, along a 99.4km line between 14.59°S, 140.73°E and 15.34°S, 140.25°E within the Gulf of Carpentaria. Recently born, immature and adult sized snakes provide the first evidence of a resident breeding population in northern Australian waters. □ *Sea snake, Gulf of Carpentaria, breeding, Pelamis.*

Colin J. Limpus, P.O. Box 541, Capalaba 4147, Australia; 10 April 2000.

The Yellow-bellied Sea Snake, *Pelamis platurus*, is widely distributed in Australia as beach-washed specimens but is poorly documented in its marine habitat (Cogger, 1975; Guinea, 1992). Shuntov (1972) implied that *P. platurus* in northern Australian waters were transported from the Coral Sea, whereas Guinea (1992) suggested they could be 'part of a geographically discrete, yet seldom encountered, breeding population'.

METHODS

Observations of sea snakes were made from the bow of the *One and All*, a twin masted, square rigged, 42.7m brigantine under sail en route from Weipa to the Wellesley Group. A bow watch during daylight hours recorded marine reptiles, mammals and birds. With each sighting, a latitude, longitude and water depth (corrected for depth of sensor below the waterline) were recorded from the ship's navigational instruments. No animals were captured. Surface water was sampled by casting a bucket over the side and hauling it in quickly, for an immediate recording of water temperature using a quick reading, mercury in glass thermometer ($\pm 0.1^{\circ}\text{C}$). All species identifications were made by the author while crew members assisted in locating wildlife. The uniquely conspicuous colouration of *P. platurus* (Heatwole, 1975a) contributed to the ease of identification.

RESULTS

A total of 112 sea snakes were seen in the 6 days. Of these 84 (75.0%) were *P. platurus*. All *P. platurus* were observed on 13 July 1992, along a 99.4km line between 14.59°S, 140.73°E and 15.34°S, 140.25°E (Table 1). All sightings occurred between 0936-1730hr. TL estimates for

32 *P. platurus* that passed close to the bow ranged from 25-60cm with 88% <45cm. At locations where *P. platurus* was recorded, mean water depth was 47.6m (SD=1.04, range=43-49m, n=35) and mean surface water temperature was 24.7°C (SD=0.05, range=24.7-24.8°C, n=6). Most *P. platurus* did not dive on close approach of the ship.

Other species of sea snakes were more difficult to identify, often because they dived on the ship's approach. Of the 28 non-*Pelamis* sea snakes observed (Table 1), only 3 *Lapemis hardwickii*, including a copulating pair, 6 *Hydrophis elegans* and 1 *Disteira kingii* were identified.

On the transect with *P. platurus* were post hatchling marine turtles *Chelonia mydas* and *Natator depressus* with carapace length ~15cm. While it is well documented that *P. platurus* and post hatchling marine turtles aggregate along drift lines where currents converge (Kropach, 1975; Carr, 1987), there were no signs (floating debris) in this case, of a convergence zone.

DISCUSSION

P. platurus is the most widely distributed sea snake species globally, with records extending from Possiet Bay in southern Siberia to New Zealand and Tasmania and from the Cape of Good Hope to Panama (Minton, 1975). However, the species rarely inhabits waters <20°C and its upper lethal temperature for indefinite survival is ~33°C (Dunson & Ehlert, 1971); while it is tolerant of low salinities, it does not occur in coastal waters subject to high variability in salinity (Dunson & Ehlert 1971). Cogger (1975) postulated a permanent breeding population off central NSW coast where surface waters reach 17°C in winter. However, Hecht et al. (1974) identified the 26°C isotherm as delimiting the

TABLE 1. Description of transects over which searches for sea snakes were conducted from the tall ship *One and All* in the Gulf of Carpentaria during 12-22 July 1992.

Date	Start				Finish				Transect length	Sea snakes sighted	
	time	latitude	longitude	depth	time	latitude	longitude	depth		<i>P. platurus</i>	other species
12 July	1105hr	12.67°S	141.77°E	12.3m	1759hr	13.15°S	141.62°E	-	64km	0	4
13 July	0715hr	14.40°S	140.87°E	48m	1800hr	15.40°S	140.23°E	43m	130km	84	16
14 July	0930hr	16.62°S	139.83°E	23m	1100hr	16.50°S	139.84°E	23m	15km	0	0
17 July	1440hr	16.08°S	139.20°E	27m	1855hr	15.56°S	139.13°E	48m	63km	0	3
18 July	0730hr	14.43°S	138.33°E	58m	1850hr	13.62°S	136.93°E	28m	177km	0	5
22 July	1031hr	12.07°S	136.77°E	20m	1200hr	11.87°S	136.75°E	35m	22km	0	0

distribution of permanent breeding colonies. *P. platurus* is a pelagic sea snake that aggregates in association with slicks and drift lines (Dunson, 1975). Aggregations are not seasonal although calm weather favours their formation (Kropach, 1975). *P. platurus* is piscivorous, in the top 2m rather than at the bottom like most sea snakes (Kropach, 1975); has been recorded diving to c. 20m (Kropach, 1975) and can adjust buoyancy to suit activities (Graham et al. 1975); cannot regain the sea if beach-washed (Dunson, 1975).

In the Gulf of Panama *P. platurus* has: TL at birth = 22-26cm; ♂♂ sexually mature at TL ~50cm; ♀♀ sexually mature at TL ~64cm; non-seasonal breeding (Kropach, 1975). By analogy, the eastern Gulf of Carpentaria population encompassed all size ranges from recently born to adult, with the majority being immature, thus demonstrating a breeding population, the first recorded for northern Australia.

Although sea snakes have been well studied in the Gulf of Carpentaria *P. platurus* has rarely been reported (Guinea, 1992; Shuntov, 1972; Heatwole, 1975b; Wassenberg et al., 1994).

The Gulf of Carpentaria is in a region that Hecht et al. (1974) predicted should support a permanent breeding colony, although its water was slightly cooler than identified as limiting permanent breeding populations. The extent and habits of this population are yet to be determined.

ACKNOWLEDGMENTS

Penny van Oosterzee and Noel Preece of Discovery Ecotours provided the opportunity to participate in the expedition and provided logistical support. The crew and guests assisted in data collection. This assistance is appreciated.

LITERATURE CITED

- CARR, A. 1987. Impact of non degradable marine debris on the ecology and survival outlook of sea turtles. *Marine Pollution Bulletin* 18(6B): 352-6.
- COGGER, H.G. 1975. Sea snakes of Australia and New Guinea. Pp. 59-140. In Dunson, W.A. (ed.) *The biology of sea snakes*. (University Park Press: Baltimore).
- DUNSON, W.A. 1975. Adaptations of sea snakes. Pp. 3-20. In Dunson, W.A. (ed.) *The biology of sea snakes*. (University Park Press: Baltimore).
- DUNSON, W.A. & EHLERT, G.W. 1971. Effects of temperature, salinity and surface water flow on the distribution of the sea snake *Pelamis*. *Limnology and Oceanography* 16: 845-53.
- GRAHAM, J.B., RUBINOFF, I. & HECHT, M.K. 1975. Temperature physiology of the sea snake *Pelamis platurus*. An index of its colonisation potential in the Atlantic Ocean. *Proceedings of the National Academy of Sciences* 68: 1360-3.
- GUINEA, M.L. 1992. The yellow-bellied sea snake *Pelamis platurus* in the Northern Territory. *Northern Territory Naturalist* 13: 37-39.
- HEATWOLE, H. 1975a. Predation on sea snakes. Pp. 233-250. In Dunson, W.A. (ed.) *The biology of sea snakes*. (University Park Press: Baltimore).
- 1975b. Sea snakes of the Gulf of Carpentaria. Pp. 145-50. In Dunson, W.A. (ed.) *The biology of sea snakes*. (University Park Press: Baltimore).
- HECHT, M.K., KROPACH, C. & HECHT, B.M. 1974. Distribution of the yellow-bellied sea snake, *Pelamis platurus*, and its significance in relation to the fossil record. *Herpetologica* 30: 387-396.
- KROPACH, C. 1975. The yellow-bellied sea snake, *Pelamis*, in the eastern Pacific. Pp. 185-216. In Dunson, W.A. (ed.) *The biology of sea snakes*. (University Park Press: Baltimore).
- MINTON, S.A. 1975. Geographic distribution of sea snakes. Pp. 21-32. In Dunson, W.A. (ed.) *The biology of sea snakes*. (University Park Press: Baltimore).
- SHUNTOV, V.P. 1972. Sea snakes of the North Australian Shelf. *Soviet Journal of Ecology*, New York 2(4): 338-44. Translation of 1971 paper in *Ekologiya* 4: 65-72.
- WASSENBERG, T.J., SALINI, J.P., HEATWOLE, H. & KERR, J.D. 1994. Incidental capture of sea snakes (Hydrophiidae) by prawn trawlers in the Gulf of Carpentaria, Australia. *Australian Journal of Marine and Freshwater Research* 45: 429-43.

THE LOGGERHEAD TURTLE, *CARETTA CARETTA* IN QUEENSLAND: FEEDING ECOLOGY IN WARM TEMPERATE WATERS

COLIN J. LIMPUS, DEIDRÉ L. DE VILLIERS, MICHELE A. DE VILLIERS,
DUNCAN J. LIMPUS AND MARK A. READ

Limpus, C.J., de Villiers, D.L., de Villiers, M.A., Limpus, D.J. & Read, M.A. 2001 06 30: The loggerhead turtle, *Caretta caretta* in Queensland: feeding ecology in warm temperate waters. *Memoirs of the Queensland Museum* 46(2): 631-645. Brisbane. ISSN 0079-8835.

Gut contents and faecal samples from 53 loggerhead turtles, *Caretta caretta*, from the Bundaberg coast, Hervey Bay, Sandy Straits, Moreton Bay and Gold Coast regions of southern Queensland continental shelf waters were examined. *C. caretta* in these coastal waters are carnivorous, consuming at least 94 taxa of benthic and near benthic organisms. Large immature and adult *C. caretta* are specialised for feeding on slow moving, hard bodied invertebrate prey with molluscs and crustaceans being the most commonly consumed taxa. Four feeding methods were identified for these *C. caretta*. The specific prey species selected was a function of the turtle's feeding area rather than its sex or size. As individuals their diet is unpredictable with some variability in the diet being attributed to individual preference. □ *Loggerhead turtle, Caretta, feeding ecology, southeast Queensland.*

Colin J. Limpus, Michele A. De Villiers, Duncan J. Limpus, *Queensland Parks and Wildlife Service, P.O. Box 155 Brisbane, 4002*; Deidré L. De Villiers, *Queensland Parks and Wildlife Service, P.O. Box 5116, Daisy Hill, 4127*; Mark A. Read, *Queensland Parks and Wildlife Service, P.O. Box 5391, Townsville M.C., 4810, Australia*; 8 May 2000.

The loggerhead turtle, *Caretta caretta*, is carnivorous and feeds on a very wide range of prey species. While it preys primarily on benthic invertebrates such as crustaceans, bivalves and gastropods, it consumes many other taxa including jellyfish, sea pens, sea urchins, holothurians, tunicates, and fish (Bleakney, 1967; Burke & Standora, 1993; Ernst & Barbour, 1989; Gudynas, 1980; Plotkin, 1996; Porter, 1972; Preen, 1996). Some of this diversity in diet is a function of the life history phase of the turtles. *C. caretta*, typical of cheloniid turtles, occupies a wide range of habitats throughout its life history (Carr, 1986; Dodd, 1988; Limpus, 1985, 1994). Eggs are laid in sandy tropical and warm temperate beaches. The hatchlings leave the beaches and disperse within days into deep water from where they enter a pelagic phase, being dispersed by ocean currents. For the first years of their life they occupy open ocean surface waters before recruiting to live in widely dispersed feeding areas over the continental shelf. Breeding adults migrate from their feeding areas to their traditional breeding sites and occupy courtship and internesting habitats within the waters adjacent to the nesting beaches for some months during each breeding season. At the completion of the breeding season they return to their respective feeding areas. Feeding by *C. caretta* is largely restricted to the pelagic phase where the young turtles utilise planktonic prey at or near the

ocean surface (Plotkin, 1996; van Nierop & den Hartog, 1984) and inshore shallow waters where the larger sized turtles feed predominantly on benthic prey (Conway, 1994; Plotkin et al., 1993; Moodie, 1979). The breeding adult does not feed while ashore for egg laying. Similarly, while in the courtship and internesting habitats, the breeding female does not feed or substantially reduces her feeding, while she is in this egg production phase (CJL unpubl. data). The hatchlings do not feed while in the nest, while crossing the beach or in the inshore waters as they disperse from the nesting beach.

The eastern Australian *C. caretta* stock (Bowen et al., 1994) is endangered with a declining breeding population (Limpus & Reimer, 1994). As part of general studies to understand their biology, we describe the diet of adult and large immature *C. caretta* feeding in inshore warm temperate waters of southeastern Queensland.

METHODS

Gut contents were obtained opportunistically from *C. caretta* from southeastern Queensland during 1989-1998. The study area extended from the Kolan River near Bundaberg (24°35'S, 152°07'E) to the Gold Coast (28°02'S, 153°26'E). Habitats utilised by *C. caretta* encompass rocky reefs, bays, estuaries and coastal open waters.

Free ranging *C. caretta* were captured during mark-recapture studies (Limpus, 1978, 1985; Limpus et al., 1994). Dead and moribund *C. caretta* were obtained through the Queensland Parks and Wildlife Service (QPWS) marine wildlife stranding program. Faecal samples were obtained from the live turtles. Digestive tract contents were obtained during necropsy of the turtles from the stranding program. The amount of gut contents collected was dependent on the state of decomposition of the carcass but, where possible, the entire alimentary tract was sampled. For each sample, the turtle's sex, age class, breeding status, midline curved carapace length (CCL), injuries, cause of death, date, and location were recorded. Carcasses were selected only if the body organs were intact. While the turtles were not feeding at the point of stranding, given the limit on state of decomposition, it is presumed that they would have fed in the adjacent waters. For ease of description, gut contents are identified by the tag number of the turtles or the museum specimen numbers. All except one sample were from non breeding turtles in or adjacent to their presumed feeding areas.

No sub-sampling was taken of large samples. Samples with fleshy biomass were fixed in 5-10% formalin solution. Samples of predominantly hard skeletal remains, including mollusc and crustacean exoskeletons, were dried and stored. Prior to sorting, samples which had been stored in formalin were rinsed in freshwater and spread on sorting trays to remove most of the moisture. Prey items from the Brachiopoda, Mollusca, Crustacea and Osteichthyes were identified to species or genus level where possible. Prey items from the Porifera, Cnidaria and Echinodermata were identified at higher taxonomic levels. No attempt was made to identify the algae and seagrass. As each prey taxon was identified, the number of individuals present was counted using identifying features of fragments that remained intact through the feeding and digestive process. Decapod crustaceans were counted by the number, size, and orientation (left/right) of chelae, and to a lesser extent, mandibles. The number of hinges and the orientation of valves assisted with bivalve counts. With gastropods, intact spires were the primary indicator of the number of individuals consumed, but at times, counts of opercula (e.g. *Turbo* spp., *Strombus* spp.) were more appropriate. Sand, stone, coral fragments, dead shell (identified by eroded and dull inner shell surfaces), charcoal and tree bark were treated as

incidentally ingested debris. Queensland Museum staff and private shell collectors assisted with the identification of prey items. For analysis, the samples were grouped by geographic origin: Bundaberg coast, Hervey Bay, Sandy Straits, Moreton Bay and Gold Coast. For the purposes of this analysis, a dominant prey species was defined as one comprising >5% of a sample by either the number of individual prey items present or by volume. Volume was used in the analysis of six samples where there were very large differences in the sizes of prey species (see Tables 2,4).

RESULTS

Fifty-three samples included 6 faecal samples and 47 digestive tract contents. The geographic origins of samples were the Bundaberg Coast (n = 16), Hervey Bay (Woodgate - Burrum Heads (3); Sandy Cape (2), Sandy Straits (2), Moreton Bay (22), and Gold Coast - Jumpinpin (8). Prey from at least 94 taxa representing 8 Phyla were identified (Table 1): 36 species of crustaceans, 43 molluscs (18 gastropod, 23 bivalve, 1 scaphopod, 1 cephalopod), 1 poriferan, 2 cnidarians, 1 brachiopod, 3 echinoderms, 1 urochordate, and at least 7 Osteichthyes.

Most food items were crushed and the soft tissues and some or all of the skeletal fragments ingested. A small range of items were ingested whole, including some fish, hêche-de-mer and small molluscs. The largest intact prey was a porcupine fish (Family Diodontidae, 21cm), lodged in the oesophagus, and which probably caused the death of the turtle (tag=Z1819). The smallest intact prey were the gastropod *Oliva culdania* (1.4cm) and the scaphopod *Dentalium* sp. (2.4cm), both in the same turtle, T89145. It is presumed that these shells had been ingested incidentally and not crushed when the turtles had targeted larger prey. Other taxa that were considered to be ingested accidentally were seagrass and barnacles: there were only isolated blades of seagrass in the gut contents from 4 *C. caretta*; some barnacles were attached to other targeted prey species such as portunid crabs. The greatest abundance of prey from an entire gut content was 670 individuals and the largest number of a single species was 565 *Solen vagenoides* (Chinese fingernail shell). Where there were >400 prey items occurred in a sample, they primarily consisted of a single species; 36% of samples comprised =90% of a single species and 15% of samples were made up of a single species.

TABLE 1. *Caretta caretta* prey species by regions within subtropical Queensland. The value in each cell denotes the number of turtles recorded with each prey species. The percentage range that each prey species contributed to a turtle's diet sample is shown in parenthesis. * indicates material which was considered incidental and not included in the analysis of prey species; # identified fish included: porcupine fish (*Diodon*), flathead (*Platycephalus*), bigeye (*Priacanthus*), flounder (*Pseudorhombus*), whiting (*Sillago*) and wrasse (Labridae).

Taxa	Genus/Species/Common name	Bundaberg	Hervey Bay	Sandy Straits	Moreton Bay	Gold Coast
No. turtles in sample		n=16	n=5	n=2	n=22	n=8
Phylum ARTHROPODA						
Class Cirripedia	* barnacle, unidentified	2(1.1-1.3%)	2(0.3-4.3%)	1(1.4%)	7(0.2-1.4%)	1(<1%)
Class Malacostraca						
Order Decapoda						
Infra-order Anomura						
Family Diogenidae	<i>Clibanarius</i> sp.	9(2.7-31.8%)				
	<i>Clibanarius taeniatus</i>				1(0.4%)	
	<i>Dardanus imbricatus</i>	12(5-90.6%)	1(16.7%)		1(16.7%)	
Infra-order Brachyura						
Family Calappidae	<i>Calappa</i> (?) <i>hepatica</i>	1(2.2%)				
	<i>Calappa</i> sp.	2(2.7-4.5%)				
	<i>Matuta</i> sp.		1(8.3%)			1(20%)
Family Goneplacidae	<i>Eucrate dorsalis</i>	1(0.2%)			12(0.6-100%)	
	<i>Galene bispinosa</i>				8(0.6-55%)	
	<i>Galene</i> cf <i>bispinosa</i>				1(1.6%)	
Family Leucosiidae	<i>Leucosia</i> sp.	8(0.2-7.1%)	2(7.7-8.3%)		2(12.5-16.7%)	
	<i>Myra affinis</i>	4(0.6-6.9%)	1(10%)		1(0.6%)	
	<i>Myra</i> sp.	1(1.7%)				
Family Parthenopidae	<i>Cryptopodia queenslandi</i>	5(0.1-4.5%)				
	<i>Parthenope nodosa</i>	8(0.2-31.8%)				
	<i>Parthenope</i> (?) <i>valida</i>	1(0.2%)				
Family Pinnotheridae	<i>Xenophthalmus pinnotheroides</i>		1(1.3%)			
Family Portunidae	<i>Charybdis natator</i>	3(0.5-6.9%)	1(25%)			3(2.5-20%)
	<i>Portunus pelagicus</i>	1(2.89%)	1(1.3%)		4(3.5-100%)	2(2.5-5%)
	<i>Portunus sanguinolentus</i>	4(1.4-25%)	2(25-90%)		11(0.2-50%)	3(2.5-20%)
	<i>Thalamita sima</i>				3(0.2-48.4%)	
	portunid crab, unidentified 1	1(3.8%)			3(2.38-50%)	1(5%)
	portunid crab, unidentified 2	1(0.5%)				
	portunid crab, unidentified 3	1(1.72%)				
	portunid crab, unidentified 4				1(17.5%)	
	portunid crab, unidentified 5	1(0.5%)				
Family Raninidae	<i>Ranina ranina</i>					4(1.7-40%)
Family Xanthidae	<i>Halimede ochtodes</i>	2(0.5-5.2%)				
	crab, unidentified 6	1(0.5%)				
	crab, unidentified 7	1(1.72%)				
	crab, unidentified 8	1(1.4%)				
	crab, unidentified 9				1(5%)	
	unidentified (fragment)	1(33%)			2(1-50%)	
Infra-order Penaeidae	penaeid prawn					1(<5%)
Order Stomatopoda	<i>Squilla</i> sp.				3(3.1-10%)	
Phylum BRACHIOPODA						
Family Lingulidae	<i>Lingula murphiana</i>		1(90%)			

TABLE 1 (cont.).

Taxa	Genus/Species/Common name	Bundaberg	Hervey Bay	Sandy Straits	Moreton Bay	Gold Coast
Phylum CHORDATA						
Class Ascidiacea	ascidian, unidentified				2(14.2-22.2%)	
Class Osteichthyes	fish, multiple species #	1(100%)	1(25%)		3(2.4-50%)	8(20-95%)
Phylum CNIDARIA						
Class Anthozoa						
Order Gorgonacea	sea whip, unidentified				1(20%)	
Order Actiniaria	anemone, unidentified	1(0.6%)				
Phylum ECHINODERMATA						
Class Echinoidea	sea urchin, unidentified	1(100%)			2(0.6-2.2%)	
Class Holothuroidea	bêche-de-mer, unidentified				1(5%)	
Class Stellerioidea	starfish, unidentified	1(90%)				
Phylum MOLLUSCA						
Class Bivalvia						
Order Arcoida						
Family Arcidae	<i>Anadara trapezium</i>	3(0.2-18.4)	1(6.3)	1(100)	2(60.7-100)	
Family Glycymeridae	<i>Glycymeris holsericus</i>	1(2.6)				
Order Mytiloida						
Family Anomiidae	<i>Patro australis</i>		1(25)			
Family Mytilidae	<i>Botula</i> sp. (elong. shiny mussel)	1(4.5)				
	<i>Modiolus ostentus</i>	1(100)				
	<i>Stavelia horrida</i>	1(2.6)				
	<i>Trichomya hirsuta</i>				2(18.8-100)	
Family Ostreidae	<i>Crassostrea commercialis</i>				1(10.7)	
	<i>Ostrea bresia</i>	1(0.2)				
	<i>Saccostrea commercialis</i>			1(0.7)		
Family Pectinidae	<i>Annachlamus flabellata</i>	3(1.3-33)			1(4.5)	
	<i>Amusium balloti</i>	4(0.5-30.4)				
Family Pinnidae	<i>Atrina pectinata</i>	6(0.2-63)	1(87)		2(3.6-33.3)	
Family Pteriidae	<i>Pinctada albina sugillata</i>	1(2.6)				
	<i>Pinctada fucata</i>		2(1.3-8.3)			
Family Spondylidae	<i>Spondylus wrightianus</i>	1(1.4)				
-	oyster fragment				1(5)	
Order Veneroida						
Family Carditidae	<i>Cardita incrassata</i>				1(10.7)	
Family Mactridae	<i>Mactra abbreviata</i>	1(2.6)				
Family Solenidae	<i>Solen vaginoides</i>				1(99.5)	
Family Tridacnidae	<i>Tridacna maxima</i>					
Family Veneridae	<i>Antigona lamellaris</i>	2(1.4-2.6)	1(2.6)		3(3.6-75)	
Family Crassatellidae	<i>Eucrassatella cumingii</i>	1(2.6)	1(2.6)		1(16.7)	
-	unidentified (fragment)	1(0.6)			2(0.2-0.6)	
Class Cephalopoda	octopus, unidentified					2(1.7-2.5)
Class Gastropoda						
Order Archaeogastropoda						
Family Trochidae	<i>Calthalotia indistincta</i>			1(0.7)		
	<i>Monilea callifera</i>				1(90)	
Family Turbinidae	<i>Turbo haynesi</i>	1(3.1)				

TABLE 1 (cont.).

Taxa	Genus/Species/Common name	Bundaberg	Hervey Bay	Sandy Straits	Moreton Bay	Gold Coast
Order Mesogastropoda						
Family Cerithiidae	<i>Pyrazus ebeninus</i>				1(5)	
Family Naticidae	<i>Polinices conicus</i>				1(0.2)	
	<i>Polinices didyma</i>	1(0.6)				
Family Potamididae	<i>Velacumantus australis</i>			1(98.6)		
Family Strombidae	<i>Strombus campbelli</i>	6(3.3-85.6)			1(91.1)	
Family Tonnidae	<i>Tonna tessellata</i>					1(20)
Order Neogastropoda						
Family Buccinidae	<i>Dolicholatirus thesaurus</i>	2(0.5-1.8)				
Family Fasciolarinae	<i>Fusinus colus</i>	1(0.6)				
Family Muricidae	<i>Lataxiena fimbriata</i>	1(1.2)				
Family Olividae	<i>Oliva caldania</i>	1(0.2)				
Family Volutidae	<i>Amoria maculata</i>	1(0.2)				
	<i>Cymbiolacca complexa</i>	1(0.2)				
	<i>Melo amphora</i>	1(95)				
	<i>Melo</i> sp.					1(<5)
	unidentified fragment	1(0.1)				1(5)
Class Scaphopoda						
Family Dentaliidae	<i>Dentalium</i> sp.	1(0.1)				
Phylum PORIFERA	sponge, unidentified	1(2.6)			3(7-50)	
Other	* algae	2(<1)			1(0.3)	
	* seagrass	2(<1)			4(<1)	

A faecal sample comprising both valves of the hairy mussel, *Modiolus ostentatus*, was obtained from a nesting ♀ *C. caretta* during oviposition at Mon Repos near Bundaberg (X37114). This was the only identifiable item obtained as faecal material from the many thousands of nesting females observed. This prey species was not found in any other turtle sample. Given that Bundaberg is outside the geographical distribution of this tropical bivalve species (Lamprell, 1998) and that breeding female marine turtles do not feed, or substantially reduce their food uptake, while away from their home feeding areas during their breeding migrations (C. Limpus, unpubl. data), it is highly unlikely that this food item originated from the Bundaberg coast. Hence this sample was excluded from the following analysis.

Bundaberg coast.

Fifty two species were identified in 14 *C. caretta* samples from the Bundaberg region (Table 1). The mean number of prey species per sample was 8.4 (SD=4.7, range=2-16). Of the 52 prey species only 14 (26.9%) were dominant prey items (Table 2). These *C. caretta* fed mostly on hermit crabs (12/14 individuals), gastropods

(5/14 individuals), bivalves (3/14 individuals) and small brachyuran crabs (5/14 individuals). For nine of these turtles the sample comprised many specimens of multiple species of prey. In contrast, for three individuals, a single large item (gastropod [*Melo amphora*], sea urchin and starfish, respectively) dominated the sample. One turtle had many specimens of the hermit crab, *D. imbricatus*, comprising >90% of the gut content. The dominant prey items from the Bundaberg Coast (Table 2) were benthic species that live on or superficially burrow into the substrate. These dominant prey species were slow moving with the exception of the more agile saucer scallop, *A. balloti*.

Hervey Bay.

Sixteen species were identified in the gut contents of five *C. caretta* from the Hervey Bay region (Table 1). The mean number of prey species per sample was 3.8 (SD=1.0, range=2-5). Of the 16 prey species, 12 (75%) were dominant prey items (Table 3). These *C. caretta* fed mostly on bivalves (4/5 individuals), crabs (4/5 individuals) or hermit crab (1/5 individuals) With one exception, this geographic group consumed

TABLE 2. Relative abundance by number of individuals of prey items identified in the gut contents of beach washed *Caretta caretta* (n=14) from the Bundaberg Coast. All samples were obtained from turtles that had been feeding immediately prior to their death. Relative abundance values are summarised only for those species comprising >5% of the total sample for the turtle. y' denotes that the species was present in the gut sample at less than the 5% level. Other species present at less than 5% of a gut content within all samples are not listed. * Where there was a very large difference in the size of prey items the abundance has been adjusted to reflect the relative volume of the prey species.

Tag number	N39890	N39891	N39925	N39944	N39961	N39970*	N39975
Date	14.02.94	18.02.94	07.02.94	04.02.94	15.01.94	25.01.93	12.01.93
Sex	♀	♀	♀	♀	♀	♀	♀
Maturity	Adult	Immature	Adult	Immature	Immature	Immature	Adult
Carapace length (cm)	94.7	83.5	93.5	75.5	82.0	83.0	104.5
Latitude	24°52'S	24°50'S	24°49'S	24°52'S	24°47'S	24°58'S	24°49'S
Longitude	152°29'E	152°28'E	152°27'E	152°28'E	152°26'E	152°29'E	152°28'E
Prey Items							
Mollusc, gastropod							
<i>Strombus campbelli</i>		86%		y			10%
<i>Melo amphora</i>							
Mollusc, bivalve							
<i>Ambusium balloti</i>	30%			y			51%
<i>Anadara trapezium</i>		y					
<i>Atrina pectinata</i>	y				y		
Crustacea, hermit crab							
<i>Dardanus imbricatus</i>	22%	5%	18%	70%	50%	5%	17%
<i>Clibanarius</i> sp.	29%	8%	32%	y	5%	5%	10%
Crustacea, brachyuran crab							
<i>Charybdis natator</i>				y	7%		
<i>Halimede ochtodes</i>				y	5%		
<i>Leucosia</i> sp.	y	y		y	5%		7%
<i>Myra affinis</i>	y			y	7%		
<i>Parthenope nodosa</i>	y	y	32%	7%	12%		y
Echinoderm, starfish						90%	
Echinoderm, sea urchin							
Tag number	N39979*	N39985	N39993	T85156	T89145	T89184	Z2029
Date	06.01.93	15.12.92	28.11.92	15.01.95	06.01.96	01.06.96	26.11.96
Sex	♀	♀	♂	♂	♂	♂	♂
Maturity	Immature	Immature	Immature	Immature	Immature	Immature	Immature
Carapace length (cm)	83.0	78.0	85.5	82.7	91.5	91.5	95.1
Latitude	24°48'S	24°48'S	24°47'S	24°58'S	24°40'S	24°40'S	24°43'S
Longitude	152°26'E	152°27'E	152°26'E	152°29'E	152°13'E	152°13'E	152°17'E
Prey Items							
Mollusc, gastropod							
<i>Strombus campbelli</i>		41%		30%	81%		
<i>Melo amphora</i>	95%						
Mollusc, bivalve							
<i>Ambusium balloti</i>		y					
<i>Anadara trapezium</i>				y		18%	
<i>Atrina pectinata</i>			y		y	63%	
Crustacea, hermit crab							
<i>Dardanus imbricatus</i>	5%	43%	91%	27%	11%		
<i>Clibanarius</i> sp.		9%		31%			
Crustacea, brachyuran crab							
<i>Charybdis natator</i>			y				
<i>Halimede ochtodes</i>							
<i>Leucosia</i> sp.			y	y	5%		
<i>Myra affinis</i>				y			
<i>Parthenope nodosa</i>				y	y		
Echinoderm, starfish							
Echinoderm, sea urchin							100%

few prey species, usually with only one species dominating the sample. For example, a single prey species constituted ~90% of the gut content (*A. pectinata*, *P. sanguinolentus*, or *Lingula murchiana*). The prey for this region represented a range of habitats: within the water column (fish), on or superficially burrowed within the substrate surface (*A. pectinata* and crabs) or burrowed deep within the substrate (*L. murchiana*). That 72 *L. murchiana* were the only species present in 1 sample indicates that the turtle was intentionally feeding on this cryptic species to the exclusion of other species.

Sandy Straits.

Four species were identified in the 2 gut contents from the Sandy Straits region (Table 1). The number of prey species per sample ranged 1-3. Two species (50%) were dominant prey items (Table 3). The 2 *C. caretta* had fed almost exclusively on either the gastropod *Velacumantus australis*, or the bivalve *A. trapezium*. Both prey species are epibenthic or superficially burrow.

Moreton Bay.

Thirty-four prey species were identified in 22 *C. caretta* samples from the Moreton Bay region (Table 1). The mean number of prey species per sample was 3.8 (SD=2.2, range=1-7). Of the 34 prey species, 27 (79%) were dominant prey items making up >5% of any one gut content (Table 4). The *C. caretta* in Moreton Bay had been feeding mostly on crabs (14/21 individuals), especially portunid crabs. When molluscs occurred in the sample, they were the major component of the prey (8/21 individuals) and a single species of gastropod or bivalve dominated. Other benthic animals (sea cucumber, sea urchin, sea whip, ascidian and sponge) were taken commonly and many *C. caretta* consumed a wide range of prey species. However, 8 of the 21 turtles ingested a very limited range. Six had gut contents approaching 100% of a single species of bivalve or crab; two had gut contents with a single gastropod species accounting for ~90%. The majority of the prey items were benthic species that live on or superficially burrow within the substrate, except for the bivalve *S. vagenoides* which burrows well below the surface. Most of these prey species are slow moving, although the fish and stomatopod are active species.

Gold Coast - Jumpinpin.

Ten species groups were identified in the gut contents of eight *C. caretta* from the Gold Coast - Jumpinpin region (Table 1). Of these, six (75%) were dominant prey items (Table 5). The *C.*

caretta sampled fed predominantly on small fish (8/8 individuals) with six of eight turtles consuming a diet consisting of >90% fish. While some species of fish could be recognised (Table 5) most material could not be identified and is grouped as all fish. Crabs contributed significant amounts to the overall volume of prey ingested by 2/8 individuals. A single specimen of the gastropod *Tonna tessellata* was a major component of the diet of one turtle. The principal prey items in this area were highly mobile species that live close to the substrate and in the adjacent water column (fish). A small amount of the slow moving benthic species that live on the substrate surface or superficially burrow were eaten also. There was circumstantial evidence (unpublished data, QPWS stranding database) that at least several of these turtles had been killed during fish trawling activities off this coastline. The prey items identified from these turtles are common among the 'trash fish' discarded from this trawl fishery. There is a high probability that these turtles were scavenging the water column or the substrate for discarded dead bycatch.

COMPARISON AMONG REGIONS. Molluscs and crustaceans dominated the diet of *C. caretta* in most areas but not in the Gold Coast region. However, the dominant species in the diet varied spatially. For example, on the Bundaberg coast the diet included a range of hermit crabs, a gastropod (*S. campbelli*) and a bivalve (*A. balloti*) for the major part of the diet (Table 2). The diet in Moreton Bay was dominated by a range of brachyuran crabs (not hermit crabs) and bivalves (not *A. balloti*) (Table 4). Within a localised area, many turtles displayed idiosyncratic feeding patterns, choosing to feed on individually unique suites of prey.

Over half (54.7%) of *C. caretta* in this study had consumed < 5 species of prey. The turtles from the Bundaberg region contained more prey species per sample (8.4 prey) while the turtles from Moreton Bay and Hervey Bay had similar numbers of prey (3.8 prey species per sample) (1 way ANOVA: $F_{2,38} = 9.57$; $p < 0.001$). The comparison excluded Sandy Straits because of the small sample size and the Gold Coast - Jumpinpin samples because it was impossible to count the masses of fish bone in the gut contents.

The size, sex and maturity of the sampled turtles are listed in Tables 2-5. There were 27 males and 21 females and two unsexed turtles in the study group. The prey ingested was unrelated to sex or size because there was no significant

TABLE 3. Relative abundance by number of individuals of prey items from *Caretta caretta* gut contents (G) of beach washed turtles or faecal samples (F) from captured wild turtles from Hervey Bay (n=5) and Sandy Straits (n=2) areas. All samples were obtained from turtles that had been feeding immediately prior to their death. Relative abundance values are summarised only for those species comprising >5% of the total sample for the turtle. The sample from specimen T79317 was a faecal sample. The remainder were from gut contents. Species present at less than 5% of a gut content are not listed.

Tag number	Hervey Bay					Sandy Strait	
	Q18573	T57853	-	Q22481	Z322	T79317	T22833
Date	11.01.96	25.11.95	27.01.98	19.12.96	24.09.92	13.06.95	11.06.95
Sex	♂	♂	♂	♂	♀	♀	♀
Maturity	Immature	Immature	Immature	Immature	Immature	Immature	Adult
Carapace length (cm)	79.4	80.9	95.2	83.4	104.0	71.0	94.1
Latitude	25°11'S	25°09'S	25°08'S	24°43'S	25°01'S	25°42'S	25°45'S
Longitude	152°37'E	152°37'E	152°35'E	153°12'E	153°21'E	15°55'E	152°57'E
Prey Items							
Mollusc, bivalve							
<i>Anadara trapezium</i>	6%						100%
<i>Atrina pectinata</i>			87%				
<i>Patro australis</i>		25%					
<i>Pinetada fucata</i>	y			8%			
Mollusc, gastropod							
<i>Velacumantis australis</i>						99%	
Crustacea, hermit crab							
<i>Dardanus imbricatus</i>				75%			
Crustacea, brachyuran crab							
<i>Charybdis natator</i>		25%					
<i>Leucosia</i> sp.			8%	8%			
<i>Mutata</i> sp.				8%			
<i>Myra affinis</i>					10%		
<i>Portunus sanguinolentus</i>		25%			90%		
Brachiopod							
<i>Lingula murphiana</i>	90%						
Fish, unidentified		25%					

difference in the number of prey species per gut sample between the sexes ($t=0.357$, d.f.=47, $p>0.05$) or by size of these large immature and adult-sized turtles (regression analysis: $F_{1,48}=0.005$, $p>0.25$; $r^2=0.0001$, $df=48$, $p>0.05$).

FEEDING OBSERVATIONS. *C. caretta* in eastern Australia used four modes of behaviour to locate and obtain their prey.

Mining. Some *C. caretta* in shallow soft-bottom habitats of Moreton Bay located buried infaunal prey items by 'mining' (Limpus et al., 1994; Preen, 1996). The turtles use sweeping motions of their front flippers to dig shallow meandering trenches ~1.5m wide with the advancing edge 0.3-0.45m deep. This mining action resembles the front flipper actions used during nesting behaviour when the ♀ is digging or filling in the

body pit (Bustard et al., 1975). Thick and thin shelled bivalves and polychaetes (Preen, 1996) of exposed infauna are then crushed and ingested by the turtles. While this feeding behaviour has been regularly observed in sea grass meadows of Moreton Bay, we have not observed it with *C. caretta* in sandy lagoons of the southern Great Barrier Reef. To be effective, mining requires a substrate that will not readily collapse as trenches are dug. The seagrass root-mass provides this short term stability in Moreton Bay.

Biting into substrate surface. In the southern Great Barrier Reef, some *C. caretta* feed on molluscs living within the top few centimetres of sand of coral-reef lagoon habitat (Limpus, 1978; Moodie, 1979). 'The turtle walks across the bottom biting up mouthfuls of the molluscs and sand, blowing out the latter with water before

TABLE 4. Relative abundance by number of individuals of prey items from *Caretta caretta* gut contents of beach washed turtles or faecal samples from captured wild turtles from Moreton Bay (n=21). All samples were obtained from turtles that had been feeding immediately prior to their death. Relative abundance values are summarised only for those species comprising >5% of the total sample for the turtle. 'y' denotes that the species was present in the gut sample at less than the 5% level. Samples from specimens K7489, T51210 and T53780 were faecal samples. The remainder were from gut contents. Not all species present in all samples are listed. * Where there was a very large difference in the size of prey items the abundance has been adjusted to reflect the relative volume of the species.

Tag number	J49809	J51131	J51658	J53275 *	J53276	K7489	Q10419
Date	12.09.89	4.09.90	18.01.91	22.06.91	24.06.91	29.05.97	29.09.91
Sex	♂	♀	♀	♂	♂	♀	♀
Maturity	Immature	Immature	Immature	Immature	Immature	Adult	Immature
Carapace length (cm)	90.9	62.5	77.1	97.7	86.2	91.5	74.6
Latitude	-	27°11'S	27°18'S	27°22'S	27°12'S	27°18'S	27°31'S
Longitude	-	153°02'E	153°04'E	153°23'E	153°22'E	153°22'E	153°23'E
Prey Items							
Mollusc, gastropod							
<i>Monilea callifera</i>							
<i>Pyrazus ebeninus</i>							
<i>Strombus campbelli</i>							
Mollusc, bivalve							
<i>Anadara trapezium</i>							
<i>Antigona lamellaris</i>							
<i>Atrina pectinata</i>							
<i>Cardita incrassata</i>							
<i>Eucrassatella cumingii</i>							
<i>Solen vaginoides</i>							
<i>Trichomya hirsuta</i>							
Crustacea, hermit crab							
<i>Dardanus imbricatus</i>							
Crustacea, brachyuran crab							
<i>Eucrate dorsalis</i>	12%	50%	100%	30%	16%		100%
<i>Galene bispinosa</i>				10%	12%		
<i>Leucosia</i> sp.	12%						
<i>Portunus pelagicus</i>	38%					100%	
<i>Portunus sanguinolentus</i>	38%	50%		20%	6%		
<i>Thalamita sima</i>					y		
Portunid Crab, unidentified 1					42%		
Portunid Crab, unidentified 4					18%		
Crab, unidentified 9							
Crustacea, <i>Squilla</i> sp.					y		
Echinoderm, sea urchin							
Echinoderm, bêche-de-mer							
Cnidarian, sea whip				20%			
Porifera, sponge				20%			
Urochordate, ascidian							
Fish, porcupine fish							
Fish, unidentified							

TABLE 4. (cont.).

Tag number	Q10460	T51210	T53780	T70057	T83099	X10789*	X10791
Date	23.05.92	10.11.90	30.08.90	19.09.95	30.05.95	7.10.96	17.05.96
Sex	-	♂	♀	♂	♀	♂	♂
Maturity	-	Immature	Immature	Immature	Immature	Adult	Immature
Carapace length (cm)	-	81.4	92.5	86.0	78.9	105.8	78
Latitude	27°08'S	27°21'S	27°26'S	27°15'S	27°21'S	27°25'S	27°21'S
Longitude	153°22'E	153°24'E	153°21'E	153°04'E	153°07'E	153°31'E	153°04'E
Prey Items							
Mollusc, gastropod							
<i>Monilea callifera</i>						90%	
<i>Pyrazus ebeninus</i>						5%	
<i>Strombus campbelli</i>							
Mollusc, bivalve							
<i>Anadara trapezium</i>			100%				
<i>Antigona lamellaris</i>							
<i>Atrina pectinata</i>							
<i>Cardita incrassata</i>							
<i>Eucrassatella cumingii</i>							
<i>Solen vuginoides</i>		99%					
<i>Trichomya hirsuta</i>							
Crustacea, hermit crab							
<i>Dardanus imbricatus</i>							
Crustacea, brachyuran crab							
<i>Eucrate dorsalis</i>				33%	57%		25%
<i>Galene bispinosa</i>				14%	29%		55%
<i>Leucosia</i> sp.							
<i>Portunus pelagicus</i>							10%
<i>Portunus sanguinolentus</i>					10%	y	
<i>Thalamita sima</i>		y		48%			
Portunid Crab, unidentified 1	50%				y		
Portunid Crab, unidentified 4							
Crab, unidentified 9							5%
Crustacea, <i>Squilla</i> sp.				y			
Echinoderm, sea urchin							
Echinoderm, bêche-de-mer						5%	
Cnidarian, sea whip							
Porifera, sponge							
Urochordate, ascidian							
Fish, porcupine fish							
Fish, unidentified	50%				y		

crushing and swallowing the shells' (Limpus, 1978).

Picking off the substrate surface. *C. caretta* will feed on visible prey items on the substrate surface. Limpus (1973) described *C. caretta* grasping, crushing and tearing a 19cm long clam, *Tridacna maxima*, from the substrate surface of a coral reef. An adult male loggerhead (CCL= 94.2cm)

was observed pulling a large distended anemone (*Stichodactyla haddoni*) from the surface of the sandy substrate on the Moreton Banks of Moreton Bay (Limpus et al., 1994). Several large immature *C. caretta* which were not engaged in 'mining' at the time have been captured while feeding on portunid crabs, *P. pelagicus*, on the bottom over the Moreton Banks (Limpus et al.

TABLE 4. (cont.).

Tag number	Z107	Z1806	Z1819 *	Z3014*	Z3057	-	-
Date	18.04.93	28.06.96	20.07.96	12.03.98	22.01.98	2.01.92	29.01.91
Sex	♂	♀	♂	♂	♂	♂	-
Maturity	Adult	Immature	Adult	Immature	Immature	Immature	Adult?
Carapace length (cm)	95.5	78.4	96	91.0	-	86.3	93.7
Latitude	26°57'S	26°57'S	27°11'S	27°14'S	27°26'S	27°23'S	27°12'S
Longitude	153°09'E	153°09'E	153° 22'E	153°11'E	153°11'E	153°12'E	153°07'E
Prey Items							
Mollusc, gastropod							
<i>Monilea callifera</i>							
<i>Pyrazus eheninus</i>							
<i>Strombus campbelli</i>					91%		
Mollusc, bivalve							
<i>Anadara trapezium</i>						61%	
<i>Antigona lamellaris</i>				75%	5%	y	
<i>Atrina pectinata</i>	33%					y	
<i>Cardita incrassata</i>						11%	
<i>Eucrassatella cumingii</i>	17%						
<i>Solen vaginoides</i>							
<i>Trichomya hirsuta</i>		100%		12%			
Crustacea, hermit crab							
<i>Dardanus imbricatus</i>	17%						
Crustacea, brachyuran crab							
<i>Euerate dorsalis</i>			35%		y		55%
<i>Galene hispidosa</i>			35%		y		15%
<i>Leucosia</i> sp.	17%						
<i>Portunus pelagicus</i>						y	
<i>Portunus sanguinolentus</i>	17%		y		y	y	15%
<i>Thalamita sima</i>							
Portunid Crab, unidentified 1							
Portunid Crab, unidentified 4							
Crab, unidentified 9							
Crustacea, <i>Squilla</i> sp.			10%				
Echinoderm, sea urchin				9%	y		
Echinoderm, bêche-de-mer							
Cnidarian, sea whip							
Porifera, sponge							7%
Urochordate, ascidian						14%	7%
Fish, porcupine fish			15%				
Fish, unidentified			y				

1994; CJL, DJL, MAR unpubl. obs.). Individual turtles may be persistent in their attempts to obtain an individual food item. For example, an adult *C. caretta* was observed for ~15 minutes as it attempted to bite a large *Trochus* sp. from a crevice in a coral boulder on Wistari Reef in the southern Great Barrier Reef. The crevice was too

narrow for the turtle's jaws to reach the mollusc. The turtle repeatedly circled and nudged the boulder apparently searching for an alternative access to the food and regularly returned to push into the crevice. *C. caretta* are occasionally captured by amateur anglers in Moreton Bay

TABLE 5. Relative abundance by number of individuals of prey items identified in the gut contents of beach washed *Caretta caretta* from the Gold Coast - Jumpinpin area (n=8). All samples were obtained from gut contents of turtles that had been feeding immediately prior to their death. Relative abundance values are summarised only for those species comprising >5% of the total sample for the turtle. 'y' denotes that the species was present in the gut sample at less than the 5% level. Not all species present in all gut contents are listed.

Tag number	-	UQ91/1533	Z3051	Z3052	Z3053	Z3054	Z3116	Z3117
Date	24.10.91	13.12.91	14.1.98	14.1.98	14.1.98	14.1.98	19.03.98	19.03.98
Sex	♂	♀	♂	♂	♂	♀	♂	♂
Maturity	Adult	Adult	Adult	Adult	Adult	Adult	Adult	Adult
Carapace length (cm)	96	97	100.5	99.7	99.5	92.7	95.8	93.6
Latitude	28°02'S	27°54'S	27°52'S	27°55'S	27°53'S	27°55'S	27°42'S	27°43'S
Longitude	153°26'E	153°24'E	153°25'E	153°25'E	153°25'E	153°25'E	153°27'E	153°27'E
Prey Items								
Mollusc, gastropod								
<i>Tonna tessellata</i>		20%						
Crustacea, brachyuran crab								
<i>Charybdis natator</i>		20%	y		y			
<i>Matuta</i> sp.	20%							
<i>Portunus sanguinolentus</i>	20%		y		y			
<i>Ranina ranina</i>	40%	20%	y		y			
Fish, mixed species including flathead (<i>Platycephalus</i> sp.), whiting (<i>Sillago</i> sp.), flounder (<i>Pseudorhombus</i> sp.), wrasse (Labridae), bigeye (<i>Priacanthus</i> sp.)	20%	40%	>90%	>95%	>90%	>95%	>95%	>90%

when the turtles ingest hooks baited with fish that lie on the bottom.

Plucking from the water column. *C. caretta* will feed within the water column (Limpus, 1978; CJL, MAR unpubl. obs.). *C. caretta* living on the reef edge at Heron Island in the southern Great Barrier Reef grazed on clusters of goose-neck barnacles, *Lepas* sp., growing on floating timber. When swarms of the jellyfish, *Pelagia noctiluca*, drifted over the coral reefs near Heron Island, adult and large immature *C. caretta* of all sizes present cease feeding on their normal food of benthic molluscs (Moodie, 1979) and rise to feed at or near the surface on these jellyfish. In contrast, *C. caretta* in Moreton Bay has not been observed to feed on the abundant *Catostylus mosaicus* within their close proximity.

In the Queensland Shark Control Program, drumlines (large hooks suspended near the surface from a float) are baited with dead fish to catch sharks (Kidston et al., 1992). *C. caretta*, especially off Point Lookout (27°26'S, 153°32'E) and the Gold Coast, regularly eat the fish baits on drumlines and are hooked. Many of these turtles have been tagged on release. Tag recoveries indicate that *C. caretta* learn to seek food from such artificial sources and return

regularly to the hooks. In an extreme case, an adult male *C. caretta* (tag T74407) was hooked at least 18 times on the baited drumlines off Point Lookout between 06 December 1993 and 09 September 1995. These turtles demonstrate that *C. caretta* will scavenge on food items floating at or near the water surface in addition to taking live food.

These four feeding modes appear to be employed by the turtles examined in the present study. The brachiopod, *L. murphiana* (Table 3), and the bivalve, *S. vaginoides* (Table 4), burrow deeply within the substrate and can occur in dense aggregations (de Villiers & Hodgson, 1993). These species can be obtained in quantity only by mining. The scallop, *A. balloti* (Table 2) and the many hermit crabs (Tables 2-4) which do not burrow would have been taken from the substrate surface. The species that burrow to only a limited extent (*A. trapezium*, *A. pectinata*, *S. campebelli*) would be obtained from beneath the surface by biting into the substrate. When a turtle scavenges discarded bycatch from trawlers (e.g. Table 5), it is simply feeding on prey items on the substrate surface or in the water column. Differences in prey encounter rate and processing may influence a turtle's choice in procuring food.

When burrowing bivalves and brachiopods were consumed in large numbers, presumably by mining, few gastropods or crabs were consumed. It would involve 'biting' as well as infaunal mining to obtain such variety. When crabs were consumed, very few, if any, bivalves were found in the gut contents. When bivalves did occur with crustaceans, it was usually superficially burrowing bivalves like the scallop *A. balloti* or razor clams *A. pectinata* that were also targeted.

Large fragments of prey exoskeleton can cause blockage of the intestine with resulting death of the turtle: T22833 (Table 3) was found floating and moribund with a necrotic large intestine blocked with a compacted mass of *A. trapezium*.

DISCUSSION

Extant turtles do not have teeth. Rather *C. caretta* has keratinised sheaths to its jaws that are specialised for grasping and fragmenting hard-bodied food items (Thompson, 1980). With marine turtles, the food is pushed from the mouth through the oesophagus to the stomach using water and a hyoid pump (Bjornadal, 1985; C. Limpus, unpubl. data). The oesophagus is lined with backwardly projecting keratinised spines that act as a filter system to allow the food to be pushed easily down the throat while impeding its return back from the stomach but not impeding the return flow of water (Thompson, 1980). The back flow of water is also used to flush sand and other small particles from the buccal cavity when the turtle bites up a mouthful of prey and sediment (Limpus, 1978). The thick, keratinised epidermal surfaces of the buccal cavity and throat provide protection to the turtles during ingestion of the sharp and abrasive surfaces of the exoskeletal fragments of molluscs and crustaceans. This thick epidermal lining to the mouth and throat also provides protection from envenomation during ingestion of venomous prey such as *Physalia* and jellyfish like *P. noctiluca*. Once the food bolus has passed beyond the oesophagus, acid secretions by the stomach would inhibit discharge of enidarian stinging cells (Sutherland, 1983). During the pelagic life history phase, the young *C. caretta* feed in surface waters (Carr, 1986). Those in later life history phases that live in the shallower inshore waters, have changed their feeding behaviour to utilise prey items on the sea floor.

The *C. caretta* in this study area were carnivorous, consuming a wide variety of benthic organisms. Prey items ranged from a single to hundreds of animals per gut sample. Quantifying

prey abundance was highly problematic as our methods give a minimum estimate of the number of each species per sample. Preen (1996) observed abundant broken mollusc shells in feeding scars left from infaunal mining, suggesting that much shell, including the identifying components, is not swallowed. Alternatively, identifiable features of prey items such as thin-toothed mollusc radula may accumulate in the gut, resulting in exaggerated numbers. For example, a count of the radulae of *S. campbelli* in sample T89145 indicated 541 individuals were consumed, yet only 21 spires were recorded from the shells retrieved. Scyphomedusae (jellyfish), hydromedusae, siphonophores and other soft-bodied macroplankton are significant prey of pelagic post-hatchling *C. caretta* (Bleakney, 1967; van Nierop & den Hartog, 1984; Plotkin et al., 1993). These soft bodied prey without skeletons are rapidly digested (Plotkin et al., 1993; van Nierop & den Hartog, 1984) and therefore, it may be difficult to identify them in gut content studies. However, many of these turtles were freshly dead and such prey items would be recognised in the anterior of stomachs if fed upon immediately prior to death. This was not the case. While the present study underestimates the occurrence of soft bodied prey, it is concluded that *C. caretta* in their non-pelagic phase does not feed extensively on large, soft-bodied planktonic organisms. Even so, the ingestion of charcoal and tree bark in some turtles suggests at least some surface feeding. It appears that when large swarms of some species of jellyfish are available, large immature and adult *C. caretta* will temporarily abandon benthic foraging in favour of plucking these items from the water column, a reversion to the feeding behaviour used during the previous pelagic phase (Erick et al., 1999). Given the finite time for food passage through the gut, a gut content or single faecal sample provides only a 'snapshot' of the diet and probably retains fewer species than were actually consumed.

C. caretta in S Queensland have unpredictable and opportunistic diets that result from selective foraging modes and chance encounters with prey patches. Our study was based primarily on stranded *C. caretta* and so foraging areas could only be approximated to broad regions. Large immature and adult *C. caretta* are specialised for feeding on slow moving, hard bodied invertebrate prey (Conway, 1994; Dodd, 1988; Plotkin et al., 1993; Moodie, 1979). As a generalised carnivore, different prey species can be expected to dominate *C. caretta* diet in different regions.

Turtles from the same locality have a common set of potential prey species yet individuals do not necessarily consume the same prey. Moodie (1979), and Conway (1994) determined in studies of the loggerheads from the southern Great Barrier Reef and the Northern Territory, respectively, that prey availability at feeding sites was different to the relative frequency of those species in the turtle gut contents. The present study also shows that individuals may feed on a very limited range of species and use specialised methods such as infaunal mining to expose the prey. Thus some variability of the diet may be attributed to individual food preference. As in the Northern Territory and GBR (Conway, 1994; Moodie, 1979) we find no correlations in diet for sex, size, season, or year. Furthermore, Moodie (1979) found that turtles foraging over the same section of coral reef were each selecting a different species of mollusc. Yet the same turtles would rise to the surface to consume jellyfish that sporadically drifted over this reef in large numbers (CJL, pers. obs.). The extent to which *C. caretta* is obtaining nutritional components via a strategy of foraging on diverse taxa or is merely optimising available food sources that can be gathered with minimum energy expenditure is not addressed herein. Brachiopods are here identified for the first time in the diet of *C. caretta*.

Fish were present in samples other than those from the Gold Coast - Jumpinpin region. Frick (1997) suggested that fish are captured alive but it is more likely that they are scavenged, especially from discarded trawler bycatch (Shoop & Ruckdeschel, 1982; Plotkin et al., 1993).

With regular trawling, there is the potential for aggregating *C. caretta* that scavenge discarded bycatch in the trawled area and hence increasing their risk of capture and death. Once the turtle is associated with a chosen area such as an interesting refuge (Limpus & Reed, 1985) or feeding on a reliable food source (feeding off baited shark hooks, this study), they can be persistent with the association despite other disturbances or human-related perturbations.

C. caretta, through their diet, has additional unquantified interactions with a number of coastal fisheries. Commercially fished species such as the sand crabs *P. pelagicus* and *P. sanguinolentus*, the spanner crab *R. ranina* and the scallop *A. balloti*, are targeted as food by some *C. caretta*. Potentially more significant to fisheries is the role of *C. caretta* in the life cycle of the ascaridoid nematode *Sulcascauris sulcata*,

a parasite of commercial scallops. *C. caretta* is the definitive host of *S. sulcata* (Sprent, 1977) with the adult worms inhabiting the stomach and intestine while eggs are shed to sea with faecal material. Molluscs are the secondary host to the larval worms and immature *S. sulcata* are frequently found in the adductor muscles of large bivalves, especially *A. balloti* (Cannon, 1978). The parasite completes its life cycle when the mollusc is eaten by *C. caretta*. This parasite can cause loss of fisheries production in areas where there is coincidence of large numbers of *C. caretta* and scallops (Lester, 1980). The occurrence of *C. caretta* off the Bundaberg coast where scallops are abundant enough to form a significant part of their diet, has the potential for maintaining locally elevated levels of infection of scallops by *S. sulcata*.

ACKNOWLEDGEMENTS

This study was a part of the Queensland Turtle Research project of the Queensland Parks and Wildlife Service. Patrick Couper (Queensland Museum), numerous QPWS staff and volunteers assisted in obtaining the diet samples. Thora Whitehead, Alan Limpus, Beverley Heidke and Kevin Lamprell provided assistance in identification and advice for molluscs. Dr Peter Davie (Queensland Museum) associated in identification of crustaceans. Two unidentified reviewers made helpful editorial comments. This assistance is gratefully acknowledged.

LITERATURE CITED

- BJORNDAL, K.A. 1985. Nutritional ecology of sea turtles. *Copeia* 1985: 736-751.
- BLEAKNEY, J.S. 1967. Food items in two loggerhead sea turtles *Caretta caretta* (Linnaeus) from Nova Scotia. *Canadian Field Naturalist* 81: 269-272.
- BOWEN, B.W., KAMEZAKI, N., LIMPUS, C.J., HUGHES, G.R., MEYLAN, A.B. & AVISE, J.C. 1994. Global phylogeography of the loggerhead turtle (*Caretta caretta*) as indicated by mitochondrial DNA haplotypes. *Evolution* 48: 1820-1828.
- BURKE, V.J. & STANDORA, E.A. 1993. Diet of juvenile Kemp's Ridley and Loggerhead sea turtles from Long Island, New York. *Copeia* 1993: 1176-1180.
- BUSTARD, H.R., GREENHAM, P. & LIMPUS, C. 1975. Nesting behaviour of loggerhead and flatback turtles in Queensland, Australia. *Proceedings Koninkl. Nederlands Akademie van Wetenschappen, Series C* 78: 111-121.
- CARR, A. 1986. New perspectives on the pelagic stage of sea turtle development. *National Oceanic and Atmospheric Administration Technical*

- Memorandum, National Marine Fisheries Service Southeast Fisheries Center 190: 1-36.
- CANNON, L.R.G. 1978. A larval acsarioid nematode from Queensland scallops. *International Journal of Parasitology* 8: 75-80.
- CONWAY, S.P. 1994. Diets and feeding biology of adult Olive Ridley (*Lepidochelys olivacea*) and Loggerhead (*Caretta caretta*) sea turtles in Fog Bay (N.T.). Unpubl. thesis, Northern Territory University, Darwin.
- DE VILLIERS, C.J. & HODGSON, A.N. 1993. The filtration and feeding physiology of the infaunal estuarine bivalve *Solen cylindraceus* Hanley 1843. *Journal of Experimental Marine Biology and Ecology* 167: 127-142.
- DODD, K. 1988. Synopsis of the biological data on the loggerhead sea turtle *Caretta caretta* (Linnaeus 1758). Fish and Wildlife Service, U.S. Department of Interior Biological Report 88(14): 1-110.
- ERNST, C.H. & BARBOUR, R.W. 1989. *Turtles of the World*. (Smithsonian Press: Washington DC.)
- FRICK, M. 1997. *Lepidochelys kempi* (Kemp's Ridley) *Caretta caretta* (Loggerhead) and *Malaclemys terrapin centrata* (Carolina Diamondback Terrapin). Diet and predation. *Herpetological Review* 28: 149.
- FRICK, M.G., QUINN, C.A. & SLAY, C.K. 1999. *Dermochelys coriacea* (leatherback sea turtle), *Lepidochelys kempi* (Kemp's ridley sea turtle), and *Caretta caretta* (loggerhead sea turtle). Pelagic feeding. *Herpetological Review* 30: 165.
- GUDYNAS, E. 1980. Notes on the sea turtles of Uruguay. *ASRA Journal* 1: 69-76.
- KENNELLY, S.J. & WATKINS, D. 1994. Fecundity and reproductive period, and their relationship to catch rates of spanner crabs, *Ranina ranina*, off the east coast of Australia. *Journal of Crustacean Biology* 14: 146-150.
- KIDSTON, W., DWYER, K., BUIK, A., WALDOCK, J. & ANDERSON, G. 1992. Review of the Operation and Maintenance of Shark Meshing Equipment in Queensland Waters: Report of the Committee of Enquiry. (Queensland Department of Primary Industries: Brisbane).
- LAMPRELL, K. 1998. Bivalves of Australia. Vol. 2. (Backhuis: Leiden).
- LESTER, R.J.G. 1980. Marine parasitology research aiding industry. *Australian Fisheries* October 1980: 13-14.
- LIMPUS, C.J. 1973. Loggerhead turtles (*Caretta caretta*) in Australia: food sources while nesting. *Herpetologica* 29: 42-45.
1978. The reef. Pp.187-222. In Lavery, H.J. (ed.) *Exploration North: Australia's Wildlife from desert to reef*. (Richmond Hill Press: Richmond).
1985. A study of the loggerhead turtle, *Caretta caretta*, in eastern Australia. Unpubl. PhD thesis, Zoology Department, University of Queensland.
1994. The loggerhead turtle, *Caretta caretta*, in Queensland: feeding ground selection following her first nesting season. National Oceanic and Atmospheric Administration Technical Memorandum National Marine Fisheries Service Southeast Fisheries Centre 351: 78-81.
- LIMPUS, C.J., COUPER, P.J. & READ, M.A. 1994. The loggerhead turtle *Caretta caretta*, in Queensland: population structure in a warm temperate feeding area. *Memoirs of the Queensland Museum* 37: 195-204.
- LIMPUS, C.J. & REED, P.C. 1985. The loggerhead turtle, *Caretta caretta*, in Queensland: observations on internesting behaviour. *Australian Wildlife Research* 12: 535-40.
- LIMPUS, C.J. & REIMER, D. 1994. The loggerhead turtle *Caretta caretta*, in Queensland: a population in decline. Pp. 39-59. In James, R. (compiler) *Proceedings of the Australian Marine Turtle Conservation Workshop* (Australian Nature Conservation Agency: Canberra).
- MOODIE, E.G. 1979. Aspects of the feeding biology of the loggerhead turtle (*Caretta caretta*). Unpubl. BSc Honours thesis, James Cook University of North Queensland, Townsville.
- PLOTKIN, P.T. 1996. Occurrence and diet of juvenile loggerhead sea turtle *Caretta caretta* in the North West Gulf of Mexico. *Chelonian Conservation Biology* 2(1): 78-80.
- PLOTKIN, P.T., WICKSTEN, M.K. & AMOS, A.F. 1993. Feeding ecology of the loggerhead sea turtle *Caretta caretta* in the Northwestern Gulf of Mexico. *Marine Biology* 115: 1-15.
- PORTER, K.R. 1972. *Herpetology*. (Saunders: Philadelphia).
- PREEN, A.R. 1996. Infaunal mining: a novel foraging method of loggerhead turtles. *Journal of Herpetology* 30: 94-96.
- SHOOP, C.R. & RUCKDESCHER, C. 1982. Increasing turtle strandings in the South-east United States: a complicating factor. *Biological Conservation* 23: 213-215.
- SPRENT, J.F.A. 1977. Ascaroid nematodes of amphibians and reptiles: *Sulcascaaris*. *Journal of Helminthology* 5: 379-387.
- SUTHERLAND, S.K. 1983. *Australian Animal Toxins*. (Oxford University Press: Oxford).
- THOMPSON, S.M. 1980. A comparative study of the anatomy and the histology of the oral cavity and alimentary canal of two sea turtles: the herbivorous green turtle *Chelonia mydas* and the carnivorous loggerhead turtle *Caretta caretta* (includes discussion of diet and digestive physiology). Unpubl. MSc thesis, James Cook University of North Queensland, Townsville.
- VAN NIEROP, M. M. & DEN HARTOG, J.C. 1984. A study on the gut contents of five juvenile loggerhead turtles *Caretta caretta* (Linnaeus) (Reptilia, Cheloniidae), from the south-eastern part of the North Atlantic coast, with emphasis on coelenterate identification. *Zoologische Mededelingen* 59(4): 35-54.

FIRST RECORD OF ELSMAN'S WHIPNOSE ANGLERFISH, *GIGANTACTIS ELSMANI* (LOPHIFORMES: GIGANTACTINIDAE), FROM AUSTRALIAN WATERS. *Memoirs of the Queensland Museum* 46(2): 646, 2001. - Elsmann's Whipnose Anglerfish *Gigantactis elsmanni* Bertelsen, Pietsch & Lavenberg (1981), is a meso- and bathypelagic species previously known from five specimens. The 384-mm SL holotype (ISH 1360/71) was trawled in the central Atlantic and the 283-mm SL paratype (LACM 10687-1) was caught in the eastern South Pacific. Other specimens have been recorded from Japan (Amaoka, 1984), the Sea of Okhotsk (Fedorov, 1994), and one specimen tentatively identified as this species from the South Atlantic (Bertelsen, Pietsch & Lavenberg, 1981).

Gigantactis contains 21 species (Bertelsen, Pietsch & Lavenberg, 1981), and these show extreme sexual dimorphism. The females have an elongate body, head length less than 35% SL, caudal peduncle length greater than 20% SL, and a very long illicium, greater than half the SL. The largest female grows to 40cm, whereas the largest male is only 2.2cm long. Males have highly developed sense organs that are presumably used to find females. Dermal denticles on the snout allow the male to attach to the female. Unlike some other ceratioid anglerfishes, male/female attachment in whipnose anglerfishes is not parasitic (Pietsch, 1999).

A 310mm SL female *G. elsmanni* (AMS L28742-001) was collected by Australian Museum staff on the HMAS Cook in 1989 in the Tasman Sea off Sydney, NSW (trawl start and finish coordinates: 33°52'30"S 152°39'00"E to 33°53'09"S 152°05'54"E). The specimen was collected by midwater trawl at a depth between the surface and 1800m over a bottom depth from 1700m to 4856m, and is a new record for both Australia and the SW Pacific. This is the second species of *Gigantactis* recorded from Australian waters, the first being *G. paxtoni* (Bertelsen & Pietsch, 1983).

The AMS specimen of *G. elsmanni* was fixed in formalin in 1989 and has been preserved since in 70% ethanol. The specimen has the following characters which, in combination, diagnose the species: illicial length 315mm (102% SL); esca papillae absent; dentary teeth relatively short, 9.0mm (longest 2.9% SL) in approximately 5 rows; longest caudal fin ray 90mm (29.0% SL). These characters are in agreement with the original description of the species, with the minor exception that the length of the longest dentary tooth is 2.8 vs. 2.9% SL. The characters of the esca also agree with the original description.

With specimens previously collected from the Atlantic, SL Pacific and Japan it was not surprising that this species was found in Australian waters. The known distribution of this species is here extended into the SW Pacific, increasing the likelihood that its distribution is circumglobal.

Acknowledgements

J. Leis is acknowledged for giving helpful advice on the manuscript. C. Bento and T. Trnski photographed the fish. J. Trnski compared characters of the fish with those in the original description.

Literature Cited

- AMAOKA, K. 1984. Family Gigantactinidae. Whipnoses. Pp 106-108. In Masuda, H., Amaoka, K., Araga, C., Uyeno, I. & Yoshino, T. (eds) *Fishes of the Japanese Archipelago*. (Tokai University Press: Tokyo)
- BERTELSEN, E. & PIETSCH, T.W. 1983. The Ceratioid Anglerfishes of Australia. *Records of the Australian Museum* 15: 17-66.
- BERTELSEN, E., PIETSCH, T.W. & LAVENBERG, R.J. 1981. Ceratioid anglerfishes of the family Gigantactinidae: morphology, systematics, and distribution. *Contributions in Science* (Los Angeles) 332: 1-74.

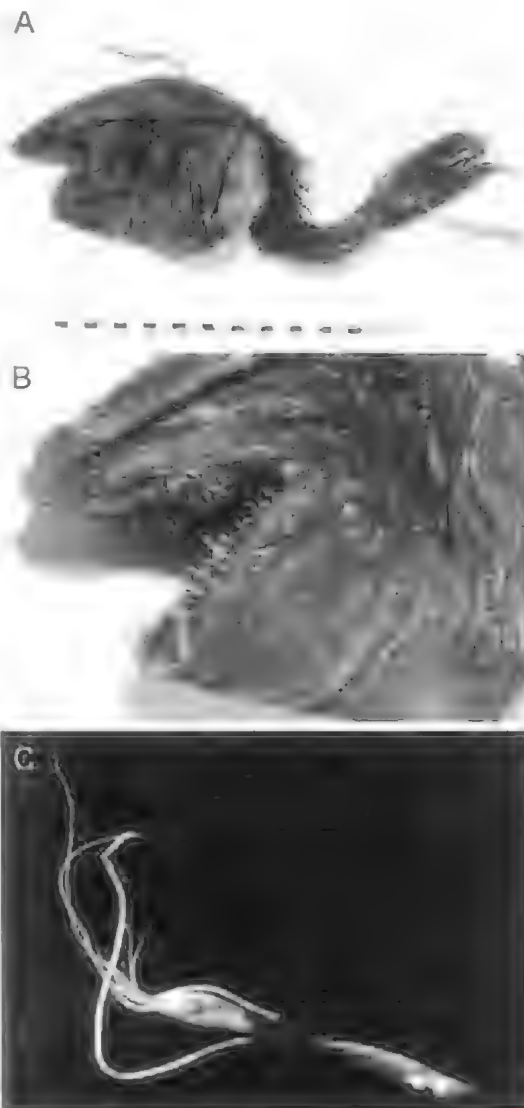


FIG. 1. A, 310mm SL female *G. elsmanni* (AMS L28742-001) collected in the Tasman Sea off Sydney, NSW; B, head (note the origin of the illicium at the tip of the snout); C, esca.

- FEDOROV, V.V. 1994. *Gigantactis elsmanni*, the first report of a species of the family Gigantactinidae (Lophiiformes) from the Sea of Okhotsk. *Voprosy Ikhtologii* 34(3): 414-415. [English translation in *Journal of Ichthyology* 34 (8): 132-133]
- PIETSCH, T.W. 1999. Gigantactinidae. Whipnose anglerfishes (deepsea anglerfishes). P. 2036. In Carpenter, K.E. & Niem, V.H. (eds) *FAO species identification guide for Fishery purposes. The Living Marine Resources of the Western Central Pacific*. Vol. 3 (FAO: Rome)

Mark A. McGrouther, Division of Vertebrate Zoology, Australian Museum, 6 College Street, Sydney 2010, 15 June 2001

AN ADDITION TO THE RAINBOWFISH (MELANOTAENIIDAE) FAUNA OF NORTH QUEENSLAND

KATRINA L. MCGUIGAN

McGuigan, K.L. 2000 06 30; An addition to the rainbowfish (Melanotaeniidae) fauna of North Queensland. *Memoirs of the Queensland Museum* 46(2): 647-655. Brisbane. ISSN 0079-8835.

A new Melanotaeniid species is described from 28 specimens collected from the Johnstone River, north Queensland. *Melanotaenia utcheensis* sp. nov. was found in sites with moderate to high water flow over cobbles and boulders and all sites are in close proximity to major agricultural activity and have moderately to highly disturbed riparian vegetation. *Melanotaenia utcheensis* sp. nov. has a distinctive colour pattern with a blue-black mid-lateral band and orange margins on vertical scale rows. It is morphologically distinct from the broadly sympatric *Melanotaenia eachamensis* (Allen & Cross, 1982) and *Melanotaenia splendida splendida* (Peters, 1866), as well as from its sister species from southern Queensland/northern New South Wales, *Melanotaenia duboulayi* (Castelnau, 1878). In particular, *M. utcheensis* sp. nov. has more first dorsal spines and fewer vertical scale rows and anal rays than *M. s. splendida*, and fewer soft second dorsal rays and more pectoral rays than either *M. eachamensis* or *M. duboulayi*. The new species is also generally smaller than either *M. s. splendida* or *M. eachamensis* and intermediate between them in eye diameter, predorsal length, head depth and body depth. □ *Melanotaeniidae*, *Melanotaenia*, rainbowfish, freshwater, North Queensland, Johnstone River.

K.L. McGuigan, Department of Zoology and Entomology, The University of Queensland, St Lucia 4072, Australia (e-mail: kmcguigan@izen.uq.edu.au); 10 May 2001.

The family Melanotaeniidae is endemic to freshwaters of Australia and New Guinea. These small rainbowfish (usually less than 12cm standard length) tend to be locally abundant, representing a major component of the freshwater fauna of the region. Rainbowfish are also popular in the aquarium trade both in Australia and overseas. There are currently 68 described Melanotaeniidae species in seven genera (Allen & Renyaan, 1998). Recent changes to taxonomy have primarily resulted from surveys in New Guinea, where fifteen species and one genus have been described since 1990 (see Allen & Renyaan, 1998). In Australia there are 4 genera with 13 species, a number that has remained static since Crowley et al. (1986) reassessed the status of southern *Melanotaenia*. *Melanotaenia* is the numerically dominant genus in Australia where it is represented by ten described species and 4 subspecies.

Some *Melanotaenia* species are geographically restricted while others are widespread, occupying a range of habitats. Widespread taxa often display interpopulation variation in morphology and colouration, making classification difficult. Intraspecific phenotypic variation is recognised in the aquarium trade where rainbowfish are sold as types, usually named for the collection locality. *Melanotaenia*

splendida splendida (Peters, 1866) is one such widespread taxon (Cape York Peninsula to Gladstone) that is sold as several types due to variation among populations in both colour and morphology.

The high level of intraspecific variation in *M. s. splendida* has caused confusion over the status of the geographically restricted and poorly characterised *Melanotaenia eachamensis* (Allen & Cross, 1982) (Crowley & Ivantsoff, 1991; Zhu et al., 1994, 1998; Pusey et al., 1997). Pusey et al.'s (1997) study of morphological variation of rainbowfish in the region supported separate species status for *M. eachamensis*. Mapping the distribution of and determining the relationship among mtDNA lineages on the Atherton Tablelands confirmed the species status of *M. eachamensis* (Zhu et al., 1994, 1998). Several of the *M. eachamensis* populations identified by Pusey et al. (1997) represented new lower altitudinal limits for the species (Rankin, Fisher and Utchee Creeks). However, subsequent mtDNA analysis of fish from those sites indicated that they represented a distinct lineage, more closely related to the southern species, *Melanotaenia duboulayi* (Castelnau, 1878) and *M. fluviatilis* (Castelnau, 1878) than to *M. eachamensis* (McGuigan et al., 2000; fig. 1). MitDNA analysis of high altitude populations not

previously characterised for morphology revealed another unique lineage, closely related to that observed in Rankin, Fisher and Utchee Creeks (McGuigan et al., 2000: fig. 1). These lineages exhibit divergences from described species consistent with a cessation of gene flow between one and two myr ago (McGuigan et al., 2000).

The status of the Utchee Creek population has been debated previously. It is sold in the aquarium trade as the Utchee Creek Type. Leggett & Merrick (1987) considered the population to be banded rainbowfish (*Melanotaenia trifasciata* Rendahl, 1922), which they resemble in colour pattern. Allen & Cross (1982) identified fish from Utchee Creek as a population of *M. s. splendida* with unusual colouration but conceded the possibility that they represented an undescribed species. In his rainbowfish classification scheme Schmida (1997) distinguished the Utchee Creek Type from all described species and, as did McGuigan et al. (2000), placed it in a group containing *M. eachamensis*, *M. duboulayi* and *M. fluviatilis*, along with *M. s. australis* populations from Western Australia.

This paper describes *M. utcheensis* sp. nov. from Utchee, Fisher and Short Creeks in the Johnstone River, north Queensland. The new species is compared to the broadly sympatric *M. eachamensis* and *M. s. splendida* and also to its sister species, *M. duboulayi*.

MATERIALS AND METHODS

SPECIMEN COLLECTION. *Melanotaenia eachamensis*, *M. s. splendida* and *M. utcheensis* sp. nov. were collected during 1998 and 1999 from sites in northeast Queensland (Fig. 2) using dip nets and traps. *Melanotaenia duboulayi* were collected in the same manner from Kholo Creek (Brisbane River) and Amamoor Creek (Mary River) in southeast Queensland (Fig. 2). Information on land use, riparian vegetation, substrate, and channel characteristics was collected at each site. Fish were transported to The University of Queensland, Brisbane and held in 72L tanks at 26°C until processing.

MORPHOLOGICAL CHARACTERISATION. The definition of characters and the format of the description follows Allen & Renyaan (1998). Morphological characterisation was performed on anaesthetised live fish (1:10000 MS222, Sigma Chemical Company). Fin ray and scale row counts were made using a light microscope. Morphometric measurements were made on microscope images using Video Trace (Leading

Edge Pty Ltd, 1994); a program that facilitates calibrated measurement directly from a live video feed. Type specimens were then euthanased by anaesthetic overdose and deposited at the Queensland Museum.

Data analysis was conducted using SPSS for Windows v. 9 (SPSS Inc., 1999). Meristic data was non-normally distributed, and could not be normalised through standard transformations. A Kruskal-Wallis test was conducted on all meristic variables and the sequential Bonferroni technique (Rice, 1989: $\alpha=0.05$, $k=7$) used to control for group-wide type-I error. Variables that remained significant after correction were subject to a non-parametric multiple comparison test with unequal sample sizes (Zar, 1984) to determine whether the significant result was due to *M. utcheensis* sp. nov. The same technique was used to assess the meristic similarity of *M. eachamensis* and *M. s. splendida*.

Morphometric data was natural log transformed. To allow comparison of shape without the confounding effect of size (as indexed by standard length) data were size corrected using the formula:

$$\text{scaled variable} = \text{observed variable} \times \left(\frac{\text{set standard length}}{\text{observed standard length}} \right)^b$$

where b was the slope of the regression (specific for sex within population) of the observed variable on standard length; set standard length was 4.0 (=ln 55mm) as this value fell within the range of all species.

A discriminant functions analysis (DFA) was conducted on the size-corrected data with species as the discriminator. A one-way ANOVA with planned comparisons was used to compare the discriminant scores of *M. utcheensis* sp. nov. with all other species. A one-way ANOVA with planned comparisons was also used to compare *M. utcheensis* sp. nov. with all other species for univariate morphometric variables. Again, the morphological similarity between *M. eachamensis* and *M. s. splendida* was determined in the same way.

Melanotaenia utcheensis sp. nov. (Fig. 3)

ETYMOLOGY. Named for the type locality, Utchee Creek, and in recognition of the history in the aquarium trade of the Utchee Creek Type.

MATERIAL. HOLOTYPE: QM I32159, ♂, Utchee Creek, North Johnstone R. (17°38'30"S 145°56'20"E). PARATYPES: Utchee Creek, North Johnstone R. (17°38'30"S 145°56'20"E), 5 females. QM I32160-32164 inclusive; Fisher Creek, North Johnstone R. (17°34'55"S 145°53'55"E), 2 males, QM I32165 and 32166, 5 females, QM I32167-32171 inclusive; Short Creek, North Johnstone R. (17°23'00"S 145°40'00"E), 10 males, QM I32172 and 5 females, QM I32173.

DESCRIPTION. The value of the holotype is presented with the observed paratypic range in parentheses. Dorsal rays VII-1, 12 (V to VII-1, 10 to 12); anal rays I, 19 (1, 16 to 20); pectoral rays 12 (11 to 15); horizontal scale rows 10 (9 to 11); vertical scale rows 34 (32 to 35); predorsal scales 13 (13-16).

Greatest body depth 34mm (31-38), head length 36mm (34-42) both as a proportion of standard length. Greatest body width 24mm (17-28) as a proportion of body depth. Snout length 32mm (34-43), eye diameter 28mm (24-32), interorbital width 22mm (19-28), depth of caudal peduncle 25mm (20-30), length of caudal peduncle 17mm (11-18) as proportions of head length.

Upper and lower jaws are of approximately equal length, oblique with a typically abrupt bend in the premaxilla between the anterior horizontal and lateral portions; the maxilla ends in front of the anterior edge of the eye; lips are thin. Scales are arranged in regular horizontal rows and their posterior edge is slightly crenulate; predorsal scales extend to the posterior end of the interorbital; preopercle has 2 scale rows from the posterior angle to the edge of the eye.

The origin of the first dorsal fin is anterior to the anal fin origin. The depressed longest first dorsal ray (second or third from origin) reaches half way between the insertion of the first dorsal and the origin of the second dorsal in females and ranges in males from the spine to the fourth soft ray of the second dorsal. The second dorsal fin origin is posterior to the anal fin origin. When depressed the longest rays of the second dorsal fin (usually second or third from insertion) extend just past the point of insertion in females, but reach almost to the caudal fin in males. The longest rays of the anal fin (usually second or third from insertion) have a depressed length the same as those of the second dorsal. In males both the second dorsal and anal fins are elongated and show a boxy outline when extended, whereas in females the fins are rounded, giving them a more ovaloid outline when extended. Length of pelvic fins is 18mm (15-26), pectoral fins 21mm

TABLE 1. Structure matrix from the discriminant functions analysis. Superscripts denote loading rank for the 3 variables that contribute most to that function, ranging from highest loading (1) to third highest (3).

	DI 1	DI 2	DI 3
Snout Length	-0.026	0.544 ¹	0.749 ¹
Eye Diameter	0.371 ¹	0.019	0.338 ²
Head Length	-0.079	0.266	0.149
Predorsal Length	0.289	0.672 ¹	0.177 ¹
Head Depth	-0.618 ¹	0.268	0.061
Body Depth	-0.469 ²	0.589 ²	-0.104

(13-19) and caudal fin 17mm (8-19), all as a proportion of head length. The pelvic fin extends half to two-thirds of the way to the anal fin origin in females and smaller males, but reaches to the third anal soft ray in large males. Pectoral fins are rounded. The caudal fin is moderately forked.

Colour in Life. The overall body colour is silver, often with an orange cast near the midline. The head and gill region is silver to pink and fish often have an obvious reddish cheek patch. Scales tend towards purple iridescence, especially on the upper half of the body. There is an obvious orange stripe between horizontal scale rows. A typical *Melanotaenia* mid-lateral band starts dark at the tail and fades forwards, tending towards blue in males and black in females. Anal, dorsal, pelvic and caudal fins range from translucent to deep red, being most strongly pigmented in males. Anal, second dorsal and pelvic fins often have black margins, especially in males. Pectoral fins are translucent.

Colour in Alcohol. The underside is pale, generally tawny in colour. Above the mid-lateral line scales are outlined in grey, with blue tones in some specimens. Fins retain black margins, but the red in anal and dorsal fins fades to pink. Dark mid-lateral bands are retained.

Sexual Dimorphism. ♂♂ and ♀♀ are easily distinguished on the basis of external characteristics. ♂♂ tend to be more strongly pigmented than ♀♀. ♂♂ are also deeper bodied. As described above, ♂♂ have longer pelvic, dorsal and anal fins. The outline of extended second dorsal and anal fins is distinctively boxy in ♂♂ and ovaloid in ♀♀.

COMPARISONS. *Melanotaenia utcheensis* can be discriminated from *M. eachamensis*, *M. s. splendida* and *M. duboulayi* on the basis of multivariate morphology (Fig. 4). *M. utcheensis* differs from all other species on Discriminant

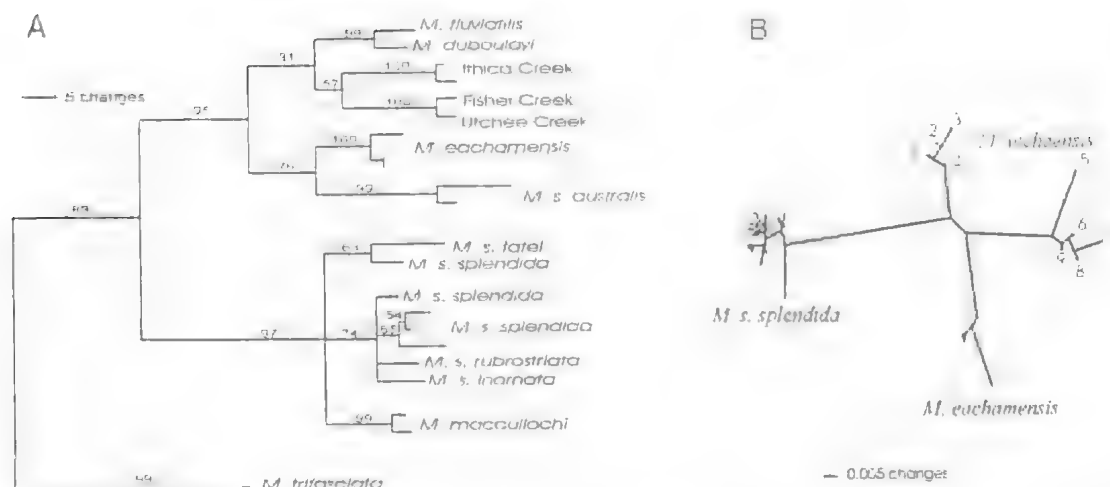


FIG. 1. A, Maximum parsimony phylogeny of mtDNA cytochrome b (351 bp) and control region (331 bp) sequence, adapted from McGuigan et al. (2000). Bootstrap support for nodes are indicated above branches. *M. utcheensis* sp. nov. represented by sequences from Ithica, Utchee and Fisher Creeks. B, Neighbour-joining network of mtDNA control region sequence (331 bp) (McGuigan & Moritz, unpubl.). Geographic locations of the nine *M. utcheensis* alleles are: 1, North Johnstone R. below the Malanda Falls; 2, Bromfield Swamp, North Johnstone R. below Malanda Falls and Ithica R.; 3, Ithica R.; 4, Ithica R.; 5, Gillies Creek; 6, Utchee Creek; 7, unnamed tributary of North Johnstone R., near Glenn Allyn; 8, Rankin, Fisher, Tregothanana and Utchee Creeks; 9, Utchee Creek.

Functions 1 (DF1) and 3 (DF3), but is distinct from only *M. duboulayi* on DF2 (one-way ANOVA with planned comparisons: $p < 0.001$ for all significant comparisons) (Fig. 4). Factor loadings indicate that negative contributions from depth variables and positive contributions from length variables dominate DF1 (Table 1). *M. eachamensis* has low scores on DF1 due to its deep body and head, and small eyes and across DF1 species are progressively shallower in head and body, and larger eyed, with *M. s. splendida* at the extreme of this trend (Fig. 4; Table 2). DF2 is determined by positive contributions from all traits (Table 1) and *M. duboulayi* is distinct on DF2 because it is generally shorter and shallower than other species (Fig. 4; Table 2). DF3 is dominated by positive contributions from snout length and eye diameter, with *M. utcheensis* having short snouts and small eyes (Table 2; Fig. 4).

Melanotaenia utcheensis was observed to be morphologically most similar to the southern species *M. duboulayi* (Table 2). This supports the mtDNA sequence data, which indicates that they are sister species (Fig. 1). *Melanotaenia utcheensis* differs from *M. duboulayi* in having fewer soft second dorsal rays and more pectoral rays, as well as a longer predorsal distance and a deeper maximum body depth (Tables 2 and 3). *Melanotaenia utcheensis* is more distinct from its

sympatric congeners *M. eachamensis* and *M. s. splendida*, differing in most of the traits measured (Tables 2 and 3). *Melanotaenia utcheensis* has fewer vertical scale rows, anal rays, and first dorsal spines than *M. s. splendida*; fewer second dorsal rays and more pectoral rays than *M. eachamensis* (Tables 2 and 3). Standard length, snout length, head length and depth, and body depth of *M. utcheensis* are less than that of *M. eachamensis*, but eye diameter is greater (Table 2). Compared to *M. s. splendida*, *M. utcheensis* has a shorter standard length, snout length, eye diameter, predorsal length and head depth, but a deeper body (Table 2). *Melanotaenia eachamensis* differs from *M. s. splendida* in having fewer vertical scale rows and anal rays, more first dorsal spines and second dorsal rays, and being shorter in standard length and predorsal length, having smaller eyes and a deeper head and body (Tables 2, 3). The intermediate position of *M. utcheensis* between *M. eachamensis* and *M. s. splendida* in both multivariate morphospace (Fig. 4) and in univariate traits (Table 2) probably contributed to the lack of previous recognition of species status.

Morphometric analyses of rainbow fish species by McGuigan et al. (2000) suggested that some characters particularly reflect phylogenetic history, while others reflect local adaptation,

TABLE 2. Mean meristic and morphometric measurement (mm) \pm standard error. All morphometric measurements (except standard length) are corrected for standard length (see equation in text). Asterix (*) indicates a significant difference between *M. utcheensis* and the asterixed species; hash (#) indicates a significant difference between *M. eachamensis* and *M. s. splendida* at $p < 0.05$ significance level (from one-way ANOVA with planned comparisons for size-corrected morphometric data and from nonparametric multiple comparisons for meristic data; see text for details).

	<i>M. utcheensis</i> (53)	<i>M. eachamensis</i> (90)	<i>M. s. splendida</i> (25)	<i>M. duboulayi</i> (40)
Vertical Scale Rows	31.72 \pm 0.27	31.67 \pm 0.15#	33.00 \pm 0.13*	32.95 \pm 0.19
Horizontal Scale Rows	9.87 \pm 0.08	10.17 \pm 0.06	10.00 \pm 0.06	10.25 \pm 0.08
Anal Rays	18.79 \pm 0.14	18.80 \pm 0.14#	20.12 \pm 0.22*	18.73 \pm 0.17
1st Dorsal Spines	5.40 \pm 0.11	5.42 \pm 0.08#	4.88 \pm 0.12*	4.95 \pm 0.12
2nd Dorsal Rays	10.79 \pm 0.09	11.91 \pm 0.12*#	10.72 \pm 0.17	11.43 \pm 0.24*
Pelvic Rays	5.96 \pm 0.04	6.02 \pm 0.04	5.00 \pm 0.00	6.00 \pm 0.00
Pectoral Rays	12.62 \pm 0.14	11.90 \pm 0.08*	12.00 \pm 0.11	11.48 \pm 0.11*
Standard Length	46.02 \pm 0.74	51.28 \pm 0.76*#	56.36 \pm 1.90*	46.18 \pm 0.88
Snout Length	3.24 \pm 0.05	3.62 \pm 0.05*	3.73 \pm 0.11*	3.10 \pm 0.08
Eye Diameter	4.56 \pm 0.05	4.37 \pm 0.04*#	5.06 \pm 0.08*	4.48 \pm 0.04
Head Length	13.36 \pm 0.10	13.68 \pm 0.10*	13.40 \pm 0.14	13.12 \pm 0.12
Predorsal Length	24.05 \pm 0.15	23.62 \pm 0.18#	25.50 \pm 0.22*	22.13 \pm 0.15*
Head Depth	12.63 \pm 0.16	14.27 \pm 0.13*#	11.37 \pm 0.20*	12.90 \pm 0.17
Body Depth	14.92 \pm 0.15	16.48 \pm 0.16*#	13.49 \pm 0.31*	14.10 \pm 0.19*

plasticity, or the effect of random genetic drift. Traits that contributed strongly to discrimination among clades in McGuigan et al.'s (2000) study (i.e. those with strong phylogenetic signal) showed the greatest differences among species in this study, strongly supporting the species status of *M. utcheensis*. Additionally, all populations included in the morphological analyses came from similar habitats (fast flowing streams in closed forest), reducing the possibility that observed differences are due to local adaptation, or phenotypic plasticity.

As documented above, historically there has been considerable confusion over species assignments in the Wet Tropics. In this study, all 3 species of the region are distinct in morphology. However, the differences between them are not pronounced and the level of variation within species suggests that none of the traits are diagnostic (Tables 2 and 3). Allen & Cross (1982) described *M. eachamensis* and indicated that it differs from *M. s. splendida* in a number of traits, including having a consistently shallower body. The opposite was observed in this study, with *M. eachamensis* being consistently deeper in the body than *M. s. splendida* (Table 2). Given the evidence of a long-term lack of gene flow (McGuigan et al., 2000), the morphological divergence between species is surprisingly limited. The lack of morphological specialisation of Australian freshwater fish has been noted

previously (McDowall, 1981), and similarity of rainbowfish in the Wet Tropics may be a related phenomenon. Despite the inconvenience such an approach would cause, I recommend that assignment of fish to species be based on multivariate morphological analyses of multiple populations, preferably with supporting molecular data (see Zhu et al., 1998).

DISTRIBUTION AND HABITAT. *Melanotaenia utcheensis* was discovered through the identification of a unique mtDNA lineage, more closely related to southern species than to other north Queensland species (McGuigan et al., 2000: fig. 1). The above analyses confirmed *M. utcheensis* as a discrete species by demonstrating that the unique mtDNA lineage correlates with a unique morphology. Morphological data for north Queensland rainbowfish is limited, such that the distribution of *M. utcheensis* might be better determined through examination of the distribution of mtDNA lineages (McGuigan & Moritz, unpubl. data; Fig. 1).

The *M. utcheensis* mtDNA lineage has been observed allopatrically in a tributary of the lower South Johnstone River (Utchee Creek) and in lower (Fisher and Rankin Creeks) and upper (Short Creek and an unnamed creek near Malanda) tributaries of the North Johnstone R (McGuigan & Moritz, unpubl. data; Fig. 2). The *M. utcheensis* mtDNA lineage was also observed

TABLE 3. The percentage of the surveyed fish that are observed to have each values of the meristic traits vertical scale rows, pectoral fin rays, first dorsal spines and second dorsal and anal soft fin rays. These traits are those observed to differ among species (Table 2).

Species	Vertical Scale Rows								Pectoral Rays					
	29	30	31	32	33	34	35		10	11	12	13	14	15
<i>utcheensis</i>	2	47	8	4	9	21	9			6	53	24	8	9
<i>eachamensis</i>	7	13	27	24	19	9	1		1	29	49	21		
<i>splendida</i>				28	44	28				16	68	16		
<i>duboulayi</i>			12	25	28	25	10		7	40	50	3		
Species	First Dorsal Fin Spines								Second Dorsal Soft Rays					
	2	4	5	6	7	5	9		10	11	12	13	14	15
<i>utcheensis</i>		8	55	28	9				36	49	15			
<i>eachamensis</i>		11	41	42	6				8	33	29	26	2	2
<i>splendida</i>		24	64	12			4	40		36	20			
<i>duboulayi</i>	3	17	60	20		2	3	15		28	30	20	2	
Species	Soft Anal Fin Rays													
	16	17	18	19	20	21	22	23						
<i>utcheensis</i>		8	30	45	9	8								
<i>eachamensis</i>	8	7	28	26	25	3	3							
<i>splendida</i>			8	16	40	32		4						
<i>duboulayi</i>		12	33	30	20	5								

at several sites in the main channel, upland (Ithica, Gillies and Williams Creeks) and lowland (Tregothanana) tributaries of the North Johnstone R (Fig. 2), admixed at various proportions with *M. s. splendida* mtDNA (Zhu et al., 1998; McGuigan & Moritz, unpubl. data). *Melanotaenia utcheensis* co-occurs, at a low frequency, with the more common *M. eachamensis* mtDNA lineage at one site, Bromfield Swamp, the headwaters of the North Johnstone River (McGuigan & Moritz, unpubl. data).

The South Johnstone River has been surveyed extensively, making it unlikely there are undiscovered populations in this drainage. However, the *M. utcheensis* lineage in so many sites in the North Johnstone River, along with the many unsampled tributaries, raises the possibility of undiscovered populations in that catchment.

Analyses of mtDNA sequence suggest that, while *M. utcheensis* and *M. eachamensis* are old species that evolved in situ, *M. s. splendida* is a young species and has colonised the region recently (McGuigan et al., 2000; Hurwood & Hughes, 2001). It is not yet clear whether the admixture of mtDNA lineages in the North Johnstone River is due to the occurrence of *M. utcheensis* and *M. s. splendida* in sympatry, or to either current or historical hybridisation. The co-occurrence of *M. eachamensis* and *M. utcheensis* at only one site, despite frequent

co-occurrence of each with *M. s. splendida*, suggests the old endemics are characterised by barriers to dispersal and gene flow; lack of geographic discontinuity suggest the barriers may be ecological. If *M. utcheensis* and *M. s. splendida* evolved allopatrically, only recently coming into contact, they may not have evolved any mechanisms that would prevent hybridisation. Freshwater fish show unusually high levels of hybridisation and introgression (Turner, 1999). A documented threat to the conservation of freshwater fish is loss of genetic identity through introgressive hybridisation with introduced taxa (Berrebi, 1997). In many cases hybridisation is facilitated by modification of habitat and human-mediated species introductions; conditions that are met in N Qld.

Within *M. utcheensis* there are 2 MtDNA lineages, 1 on the Atherton Tablelands (e.g., Short Creek) and 1 primarily in the lowlands (e.g., Utchee Creek) (McGuigan et al., 2000: fig. 1). The presence of these sister lineages with a highly structured geographic distribution suggests long-term barriers to gene flow, and considerable antiquity of the endemic lineage. With additional information on ecology and interactions of rainbowfish in the Wet Tropics, it may become appropriate to accord species status to these 2 lineages, which are differentiated morphologically (McGuigan, unpubl. data). Lacking

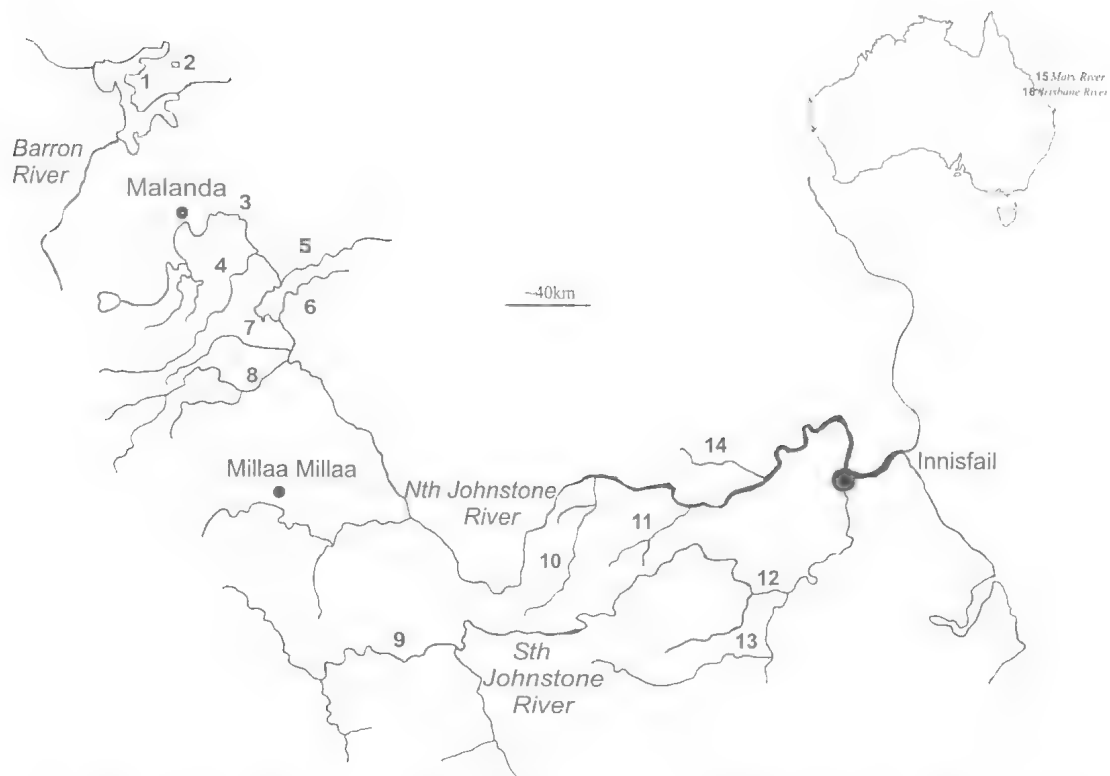


FIG. 2. Distribution of *Melanotaenia* species as determined from the distribution of mtDNA lineages (McGuigan & Moritz, unpubl. data). Sites sampled in this study indicated with *: 1, Tinaroo Dam (*M. s. splendida*: 17°09'30"S 145°35'10"E); 2, Lake Euramoo (*M. eachamensis*: 17°09'30"S 145°37'40"E); 3, Upper North Johnstone R. (*M. s. splendida*: 17°30'30"S 145°37'20"E); 4, Ithica R. (*M. utcheensis*: 17°24'25"S 145°37'10"E); 5, * Short Ck (*M. utcheensis*: 17°23'00"S 145°40'00"E); 6, unnamed tributary (*M. utcheensis*: 17°23'50"S 145°39'20"E); 7, Gillies Ck (*M. utcheensis*: 17°25'40"S 145°36'15"E); 8, * Dirran Ck (*M. eachamensis*: 17°28'30"S 145°32'53"E); 9, * Upper South Johnstone R. (*M. eachamensis*: 17°39'25"S 145°42'55"E); 10, Rankin Ck (*M. utcheensis*: 17°34'15"S 145°53'55"E); 11, * Fisher Ck (*M. utcheensis*: 17°34'55"S 145°53'55"E); 12, * Lower South Johnstone R. (*M. s. splendida*: 17°43'50"S 145°56'00"E); 13, * Utchee Ck (*M. utcheensis*: 17°38'30"S 145°56'20"E); 14, Tregothanana Ck (*M. utcheensis*: 17°31'20"S 145°57'30"E); 15, * Amamoor Ck (*M. duboulayi*: 26°21'S 152°40'E) and; 16, * Kholo Ck (*M. duboulayi*).

such data, I have taken the conservative approach of recognising both lineages as a single species.

Melanotaenia utcheensis is found in moderate to fast flowing water, in sections of stream consisting of deep pools separated by short runs. The substrate consists of cobbles and boulders with little fine sediment. Most sites have good visibility, but Rankin Creek and the lower North Johnstone main channel have very poor visibility due to large amounts of suspended solids. Visibility varies substantially across time, probably due to seasonal changes in land use and rainfall. Utchee Creek is the most structurally complex site with exposed root masses and overhanging vegetation. Other sites have undercut banks or grass beds. Sampled sites in

Fisher, Utchee and Ithica Creeks have a riparian buffer zone dominated by native vegetation. Other sites have highly disturbed riparian vegetation (completely absent or dominated by exotic species). These sites are located in agricultural lands such as banana and tea plantations.

Melanotaenia utcheensis commonly co-occurs with purple spotted gudgeons (*Mogurnda adspersa*), long finned eels (*Anguilla reinhardtii*) and less commonly with blue-eyes (*Pseudomugil signifer*), roman nosed gobbies (*Awaous acritosis*), swamp eels (*Ophisternon* sp.), grunTERS (*Hephaestus* sp.) and exotic guppies (*Poecilia reticulata*) (pers. obs.; B. Pusey, pers. comm.).

The Wet Tropics of north Queensland are listed



FIG. 3. *Melanotaenia utcheensis*, ♂, Utchee Creek, South Johnstone R., northeast Queensland.

as a World Heritage area, partly in recognition of the high level of endemism. As yet, there is little known about this most recent addition to the endemic fauna, *M. utcheensis*. The geographic separation of populations of *M. eachamensis* and *M. utcheensis*, and the structure of genetic diversity within the latter, suggest a distribution that has been stable over a long period. It is not yet clear what the mixed populations of *M. s. splendida* and *M. utcheensis* represent. Pure *M. utcheensis* populations are currently known from only five sites (Fig. 2), with stream structure suggesting a restricted area of occupancy at those sites. Observations on population size during sampling suggested that population size was fewer than 1,000 mature individuals per site. If the mixed populations of *M. s. splendida* and *M. utcheensis* represent different stages in an ongoing exclusion of *M. utcheensis* through competition, predation or introgressive hybridisation, *M. utcheensis* would qualify as vulnerable under the criteria of the World Conservation Union. *M. eachamensis* is infamous as the first Australian freshwater fish to be declared extinct (in the wild). Although it has been rediscovered in the wild (Zhu et al., 1998), its disappearance from Lake Eacham is a strong warning for management of freshwater fish. Circumstantial evidence suggests that the cause of the demise of *M. eachamensis* in Lake Eacham

was the introduction of 4 non-endemic piscivorous species (Barlow et al., 1987). In addition to the threat of predation, the potential for loss of genetic identity through hybridisation, at the population and species levels, should be considered in formulation of management strategies. Translocation of fish, either deliberately, or accidentally as a by-product of general water movement, or as live bait for fishing, has the potential to impact severely on diversity.

ACKNOWLEDGEMENTS

DPI Walkamin, Brad Pusey, Geoff Carey, David Hurwood, Brian Stumer, Adam Fletcher, Laura Paetkau, Kym Collins, Lisa Pope, Craig Franklin, Craig Moritz and Culum Brown assisted in collection. This paper benefited from the input of Walter Ivantsoff, Culum Brown, Craig Moritz, Craig Franklin, Mark Blows, Elizabeth O'Brien and Lisa Pope. This paper is an outcome of a research project on rainbowfish funded by an ARC grant to Craig Moritz.

LITERATURE CITED

- ALLEN, G.R. & CROSS, N.J. 1982. Rainbowfishes of Australia and Papua New Guinea. (Angus & Robertson: Sydney).
 ALLEN, G.R. & RENYAAN, S.J. 1998. Three new species of rainbowfishes (Melanotaeniidae) from Irian Jaya, Indonesia. *aqua, Journal of Ichthyology and Aquatic Biology* 3: 69-80.

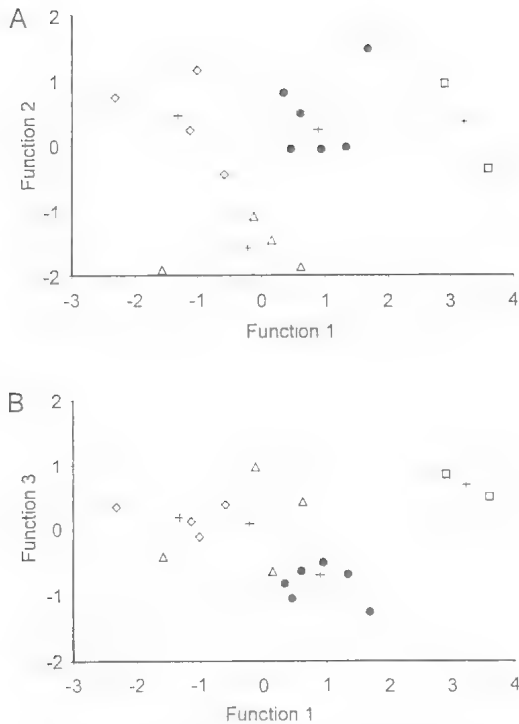


FIG. 4. Mean score for ♂s and ♀s of each population on: A, functions 1 and 2; and B, functions 1 and 3 of the Discriminant Functions Analysis. (◇ *M. eachamensis*, □ *M. s. splendida*, △ *M. duboulayi*, ● *M. utcheensis*, + group centroids).

- BARLOW, C.G., HOGAN, A.E. & RODGERS, L.J. 1987. Implication of translocated fishes in the apparent extinction in the wild of the Lake Eacham rainbowfish, *Melanotaenia eachamensis*. Australian Journal of Marine and Freshwater Research 38: 897-902.
- BERREBI, P. 1997. Species introduction in freshwater environments: Genetic impacts. Bulletin Francais de la Peche et de la Pisciculture 344-45: 471-487.
- CASTELNAU, F.L. 1878. On several new Australian (chiefly) freshwater fishes. Proceedings of the Linnean Society of New South Wales 3: 140-144.
- CROWLEY, L.E.L.M., IVANTSOFF, W. & ALLEN, G.R. 1986. Taxonomic position of two crimson-spotted rainbowfish, *Melanotaenia duboulayi* and *Melanotaenia fluviatilis* (Pisces: Melanotaeniidae) from eastern Australia, with special reference to their early life-history stages. Australian Journal of Marine and Freshwater Research 37: 385-398.
- CROWLEY, L.E.L.M. & IVANTSOFF, W. 1991. Genetic similarity among populations of

rainbowfishes (Pisces: Melanotaeniidae) from Atherton Tableland, Northern Queensland. Ichthyological Exploration of Freshwaters 2: 129-137.

- HURWOOD, D. & HUGHES, J. 2001. Interdrainage dispersal of eastern rainbowfish from the Atherton Tableland, north-eastern Australia. Journal of Fish Biology 58: 1125-1136.
- LEADING EDGE PTY. LTD. 1994. Video Trace: Image Measurement System. (Leading Edge Pty. Ltd.: Marion, South Australia).
- LEGGETT, R. & MERRICK, J.R. 1987. Australian Native Fishes For Aquariums. (Artarmon: NSW).
- McDOWALL, R.M. 1981. The relationships of Australian freshwater fishes. Pp. 1253-1273. In Keast, A. (ed.) Ecological Biogeography of Australia. (Dr W. Junk Publishers: The Hague).
- McGUIGAN, K., ZHU, D., ALLEN, G.R. & MORITZ, C. 2000. Phylogenetic relationships and historical biogeography of Melanotaeniid fishes in Australia and New Guinea. Marine and Freshwater Research 51: 713-723.
- PETERS, W.C.H. 1866. Mittheilun uber Fische. Monatsberichte der K niglichen Preussischen Akademie der Wissenschaften zu Berlin 1866: 509-526.
- PUSEY, B.J., BIRD, J., KENNARD, M.J. & ARTHINGTON, A.H. 1997. The distribution of the Lake Eacham rainbowfish in the Wet Tropics Region, North Queensland. Australian Journal of Zoology 45: 75-84.
- RENDAHL, H. 1922. A contribution to the ichthyology of north-west Australia. Meddeleser Fra det Zoologiske Museum, Kristiania 5: 163-197.
- RICE, W.R. 1989. Analysing tables of statistical tests. Evolution 43: 223-225.
- SCHMIDA, G. 1997. What's in a name anyway. Fishes of Sahul 11: 481-500.
- SPSS INC. 1999. SPSS for Windows v. 9. (SPSS Inc.: Chicago, Illinois).
- TURNER, G.F. 1999. What is a fish species? Reviews in Fish Biology and Fisheries 9: 281-297.
- ZAR, J.H. 1984. Biostatistical Analysis. (Prentice-Hall International, Inc.: New Jersey).
- ZHU, D., JAMIESON, B.G.M., HUGALL, A. & MORITZ, C. 1994. Sequence evolution and phylogenetic signal in control-region and cytochrome b sequences of rainbowfishes (Melanotaeniidae). Molecular Biology and Evolution 11: 672-683.
- ZHU, D., DEGNAN, S. & MORITZ, C. 1998. Evolutionary distinctiveness and status of the endangered Lake Eacham rainbowfish (*Melanotaenia eachamensis*). Conservation Biology 12: 80-93.

SEA SPIDERS (PYCNOGONIDA) FROM THE GREAT BARRIER REEF, AUSTRALIA, FEED ON FIRE CORALS AND ZOANTHIDS. *Memoirs of the Queensland Museum* 46(2): 656. 2001. Tropical sea spiders have been scarcely studied and associations between pycnogonids and reef organisms are rarely reported. The possibility of sea spiders feeding on scleractinian corals had been suggested once (Child, 1998) but no evidence had been presented for either fire corals or zoanthids as prey of sea spiders before.

This note reports the occurrence and feeding activity of the pycnogonid *Endeis mollis* on the fire coral *Millepora exaesa* (Class Hydrozoa) and species of Zoanthidea (Class Anthozoa) from Rib Reef, Pandora Reef and Goold Island in the central section of the Great Barrier Reef. This is the first report on coral reef sea spiders feeding activity, and is based on both field and laboratory observations.

Adults of *Endeis mollis* (32 individuals) were found on different colonies of *Millepora exaesa* (Fig. 1) at Rib Reef (6-9m depth). On several occasions, the sea spiders were observed feeding on the coral inserting the tip of the proboscis into a coral polyp and remaining attached for about 60 sec. Individuals of *E. mollis* were also observed feeding on *Palythoa caesia* and crawling on a *Parazoanthus* sp. at Rib Reef.

Related *Endeis biseriata*, was found in the reef flat of Goold Island and Pandora Reef (2-4m depth). Twenty-two adults of *E. biseriata* were found on *Protopalpythoa* sp. Similar feeding activity to that of *E. mollis* was observed in some individuals of *E. biseriata* at both sites.

The relative high number of *E. mollis* on the coral *Millepora exaesa* and of *E. biseriata* on the zoanthid *Protopalpythoa* sp. suggest a preference by the *Endeis* spp. for

these hosts, at least at the reefs visited. Observations made under captive conditions in the laboratory with the aid of a low light video camera corroborated the sequence of movements observed in the field and more importantly, the ingestion of cnidarian tissue by the sea spiders. Some pycnogonids are known to sequester and accumulate metabolites from prey, apparently to be used as defence (Sheerwood et al., 1998). It remains to be studied whether this association between *Endeis* spp. and cnidarians from the Great Barrier Reef could be chemically mediated, since *Millepora* and zoanthids in general, are known for their high concentration of toxins (Fosså & Nilsen, 1998).

Acknowledgments

Thanks to G. Díaz-Pulido for help with collecting and photography. I thank the Australian Institute of Marine Science (AIMS) for providing access to the Great Barrier Reef on board the RV Harry Messel.

Literature Cited

- CHILD, A. 1998. *Nymphon torulum*, new species and other Pycnogonida associated with the coral *Oculina varicosa* on the east coast of Florida. *Bulletin of Marine Science* 63: 595-604.
- FOSSA, S.A. & NILSEN, A.J. 1998. The modern coral reef aquarium. (Birgit Schmettkamp Verlag: Bornheim).
- SHEERWOOD, J., WALLS, J.T. & RITZ, D.A. 1998. Amathamide alkaloids in the pycnogonid, *Stylopallene longicauda*, epizoic on the chemically defended bryozoan, *Amathia wilsoni*. *Papers and Proceedings of the Royal Society of Tasmania* 132: 65-70.

Claudia P. Arango, Department of Zoology and Tropical Ecology, James Cook University, Townsville 4811; 8 November 2000.



FIG. 1. Underwater photograph of *Endeis mollis* (Pycnogonida) on the fire coral *Millepora exaesa*.

DIAGRAMMA MELANACRUM NEW SPECIES OF HAEMULID FISH FROM INDONESIA, BORNEO AND THE PHILIPPINES WITH A GENERIC REVIEW

JEFFREY W. JOHNSON, JOHN E. RANDALL AND STEPHEN F. CHENOWETH

Johnson, J.W., Randall, J.E. & Chenoweth, S.F. 2001 06 30: *Diagramma melanacrum*, new species of haemulid fish from Indonesia, Borneo and the Philippines with a generic review. *Memoirs of the Queensland* **46**(2): 657-676. Brisbane. ISSN 0079-8835.

The haemulid fish *Diagramma melanacrum* is described from 5 specimens: 1 S of Lombok, 1 off Bali, 1 off Halmahera, and 2 from Bonebetang Is., Sulawesi. The species is known also from underwater photographs at the islands of Moyo and Romang, S Indonesia, Sipadan and Mabul off NE Borneo, Tomini Bay in Sulawesi, Bohol in the Philippines and Ashmore Reef, Timor Sea. It is distinct among haemulids in having IX-X, 22-24 dorsal rays; 55-57 lateral-line scales; swimbladder with 3 small anterior projections; dorsal spine 3 or 4 longest, 1.8-2.9 in head; first dorsal spine about half length of second; pelvic fins reaching vent or slightly beyond, 1.2-1.3 in head; and in colour: pale yellow dorsally, shading through grey to whitish ventrally, with numerous small dark brown spots on head, body and dorsal fin, and caudal fin with lower fourth black; anal and pelvic fins mainly black. *Diagramma pictum* is divided into 5 geographically separate subspecies: *D. pictum pictum* (Thunberg), from the western Pacific and Indo-Malay Archipelago, excluding Australia and S New Guinea; *D. pictum labiosum* Macleay, from N Australia and S New Guinea; *D. pictum cinerascens* Cuvier, from the Bay of Bengal to the Persian Gulf; *D. pictum punctatum* Cuvier, from the Red Sea; and *D. pictum centurio* Cuvier, from East Africa. □ *Diagramma*, *Haemulidae*, *Indonesia*, *Philippines*, *generic review*.

Jeffrey W. Johnson, Queensland Museum, PO Box 3300, South Brisbane 4101, Australia (e-mail: jeffj@qm.qld.gov.au); John E. Randall, Bishop Museum, 1525 Bernice Street, Honolulu, HI 96817; Stephen F. Chenoweth, Genetics Laboratory, Faculty of Environmental Sciences, Griffith University, Nathan 4111, Australia; 18 May 2001.

Haemulid fishes of *Plectorhinchus* and *Diagramma* (commonly Thicklips, Sweetlips, Rubberlips or Slateys) are important components of the fish fauna of coral reefs and adjacent habitats of the Indo-Pacific region. Indo-Pacific species of *Plectorhinchus* (23) and *Diagramma* (2) are strikingly different in colour as juveniles, and some have intermediate phases that differ from either the juvenile or the adult. Association of juveniles to adults is still not complete for all species. Like other haemulids, *Plectorhinchus* and *Diagramma* are primarily nocturnal. They tend to form small, nearly stationary aggregations on coral reefs by day and disperse at night for feeding on a wide variety of small benthic invertebrates.

In 1988, while diving in 36m on a reef off NW Moyo Island (8°13'N, 117°30'E) in S Indonesia, one of us (JER) encountered a small group of an unknown haemulid fish that was believed to be a species of *Plectorhinchus* Lacépède. A photograph (Fig. 3D) was sent to Roland J. McKay at the Queensland Museum who reported that it appeared to be undescribed.

The Queensland Museum has a specimen of this species, taken by trawl S of Lombok in the

Lesser Sunda Islands. It had been misidentified as *P. picus* and was reported and illustrated as such (Gloerfelt-Tarp & Kailola, 1984). Burgess et al. (1988, pl. 221) followed Gloerfelt-Tarp & Kailola with their artist's impression. Re-examination of the QM specimen revealed that it has X dorsal spines (XI-XIV in species of *Plectorhinchus*) and a swimbladder with 3 small anterior projections (not known in *Plectorhinchus*). These are features of *Diagramma* Cuvier to which it is now assigned.

Additional specimens are known from Denpasar, Bali and Halmahera, Indonesia and Bonebetang Is., Sulawesi. Underwater photographs by JER at Romang Island, Indonesia (7°34'S, 127°27'E); by Klaus E. Fiedler at Sipadan Island, Sabah; by Dieter Eichler at Bohol Island, Philippines; by Rudie Kuiter at Mabul, Borneo (QMNR 44-45) and the S edge of Tomini Bay, central-eastern Sulawesi (QMNR 46-47, QMNP 200); and by J. Barry Hutchins at Ashmore Reef, Timor Sea indicate that the species is widespread in the East Indian region.

Diagramma has generally been regarded as monotypic (Smith, 1962; McKay, 1983), although Kuiter & Debelius (e.g. 1994)

recognised 2 closely related species. Apart from the species described here, 5 apparently allopatric colour forms of *D. pictum* (Thunberg) occur, with the SE Asian form most distinctive. These variants are most readily recognisable in the large juvenile to subadult colour phases. All forms have previously been assigned specific names; however, with the exception of *D. labiosum* Macleay from Australia, these species have generally been regarded as junior synonyms of *D. pictum*. Attempts were made using colour and morphometric and meristic data, as well as through analysis of mitochondrial DNA, to determine whether some of these forms represent distinct species. The results of both methods were inconclusive. DNA analysis suggested that there may be almost as much genetic divergence among widely separated Australian populations of *D. 'labiosum'* as there is between some of these populations and *D. pictum* from Singapore. From these comparisons, as well as non-genetic examination of other colour forms from the Indian Ocean, it was concluded that more detailed genetic study would be necessary. All colour varieties appear to form geographically separate populations and should be afforded interim recognition as subspecies of *D. pictum*.

METHODS

The following measurements were taken: Standard length (SL) = tip of snout (not upper lip) to base of caudal fin (hypural plate flexure); body depth = maximum depth from base of dorsal spines; body width = maximum width just posterior to gill opening; head length (HL) = tip of snout (not including upper lip) to posterior margin of opercular membrane; snout length = tip of snout (not including lip) to fleshy margin of orbit; interorbital space = least fleshy width; preorbital depth = least depth from lower edge of orbit to above end of maxilla; caudal peduncle length = rear of anal fin base to base of caudal fin; spine and ray lengths were measured to the base of these elements; diameter of spots on the body were taken from spots of most common width on the upper body.

The last ray of the dorsal and anal fins was counted as one, although divided to base; pectoral ray counts include the upper rudimentary ray; lateral-line scale counts were made to the caudal flexure and include tubed scales only; gill-raker counts were made on the first arch and include all rudiments that are at least long as wide; the upper-limb gill-raker count was given first; the lower-limb count

includes the raker at the angle. Figures for the holotype are given in parentheses. Total length (TL) is quoted where size was estimated from photographs of fish not collected, and in the key, to assist in field identification of fresh or live material. Institutional abbreviations: Australian Museum, Sydney (AM); The Natural History Museum, London (BMNH); Bernice P Bishop Museum, Honolulu (BPBM); CSIRO Marine Laboratories, Hobart (CSIRO); Museum National d'Histoire Naturelle, Paris (MNHN); Miyazaki University, Miyazaki (MUFS); Northern Territory Museum, Darwin (NTM); Phuket Marine Biological Centre, Phuket (PMBC); Queensland Museum, Brisbane (QM); JLB Smith Institute of Ichthyology, Grahamstown (RUSI); Museum für Naturkunde an der Universität Humboldt zu Berlin (ZMB).

DNA EXTRACTION, PCR AND SEQUENCING

The genetic analyses and its statistical treatment were carried out by SC. Total genomic DNA was isolated from muscle tissue using sequential phenol/chloroform extractions following digestion with Proteinase K (Sambrook et al., 1989). Two oligoprimers were used to amplify a 420bp fragment of the mitochondrial Cytochrome B gene, L 1475 (Meyer, 1991) and CB2H (Palumbi et al., 1991). PCR mixtures contained 5µl of 1.25mM dNTP's (Promega), 5µl of Promega Polymerase reaction buffer, 1 unit of Promega *taq* DNA polymerase (#1662), 5µl of MgCl₂, 2.5µl of each primer (10µM), 1µl of genomic template DNA, made up to a volume of 50µl with autoclaved distilled water and overlaid with 30µl of light mineral oil. The mixture was subjected to 35 cycles of the following thermal profile: 5min at 94°C (only on initial cycle), 30sec at 94°C, 30sec at 55°C, 1min at 72°C and 5min at 72°C (on final cycle only).

PCR-amplified DNA was then purified for sequencing using an agarose gel purification kit (QIAGEN). Light strand sequences were generated for each individual using Automated DNA Sequencing Technology (Applied Biosystems Inc.) following the manufacturers directions. Nucleotide sequences were aligned by eye and identical sequences were assigned the same haplotype number for subsequent statistical analysis.

Nucleotide diversity and nucleotide divergence statistics (Nei, 1987) were calculated within and among each pair of samples using REAP (McElroy et al., 1991). The phylogenetic relationships among haplotypes was represented

as a minimum spanning network. Minimum spanning trees were reconstructed with the aid of a program supplied by L. Excoffier.

SYSTEMATICS

Diagramma melanacrum

Johnson & Randall, sp. nov.

(Common name: Blackfin Slatery)

(Figs 1A-F, 8)

Plectorhinchus picus (non Valenciennes) Gloerfelt-Tarp & Kailola, 1984: 198 (fifth fig.), 199, 340.

Plectorhinchus picus (non Valenciennes) Burgess, Axelrod & Hunziker, 1988: pl. 221, lower right fig.

ETYMOLOGY. Greek *melanos*, black; and *akros*, tip or at the end; refers to black outer part of anal and pelvic fins and lower part of caudal fin.

MATERIAL. HOLOTYPE: QMI20291, 410mm SL, Indonesia, S of Lombok, 8°24'S, 116°01'E, trawl, T. Gloerfelt-Tarp, 1982. PARATYPES: QMI30725, 187mm SL, Indonesia, Kampung Loleba, Wasile district, Halmahera, 00°58'N, 127°56'E, trawl, H. Singou, 1/2/1979; QMI20285, 133mm SL, Indonesia, Denpasar, Bali, 8°46'S, 115°10'E, trawl, T. Gloerfelt-Tarp, 1982; BPBM 26719, (2) 219-254mm SL, Sulawesi, W side Bonebetang Is., spear, 20m, sand at reef edge, J.E. Randall, 8/9/1978. (Fig. 8).

DIAGNOSIS. Dorsal rays X-XI, 22-24; tubed lateral-line scales 55-57; outer row of teeth in jaws slightly enlarged, movable; swimbladder with 3 short anterior projections; third or fourth dorsal spine longest, 1.8-2.9 in head; first dorsal spine 1.7-2.3 in length of second; interspinous membranes of dorsal fin not incised; pelvic fins reaching vent or slightly beyond, 1.2-1.3 in head; body light yellow dorsally, shading to pale silvery grey on sides and ventrally, with numerous small dark brown spots, which are smaller and form oblique rows on body below lateral-line; head light purplish grey with numerous small brown spots, opercular membrane black; dorsal fin and upper 3/4 of caudal fin with small dark spots; lower 1/4 of caudal fin black; anal and pelvic fins mainly black. Juveniles from 133mm SL with spots about size of pupil on head, body, dorsal and caudal fins becoming progressively smaller and more numerous with age. Juveniles and subadults up to 254mm SL with narrow discontinuous wavy lines on operculum and cheeks, extending to about level of anterior margin of eye; these lines breaking up into spots in larger specimens.

DESCRIPTION. (Table 1) Dorsal rays X-XI, 22-24 (X, 22); anal rays III, 6-7 (III, 6); pectoral rays 17 (first ray rudimentary, second

unbranched); pelvic rays I, 5; tubed lateral-line scales 55-57 (56); scales above lateral-line to origin of dorsal fin 14-15 (14); gill rakers 6-7+13-14 (6+14).

Body oblong and moderately deep, depth 38.0-41.5% SL (41.5%); body compressed, width 31.6-40.8% depth (39.4%); caudal peduncle depth 10.7-11.8% SL (10.7%); caudal peduncle length 22.6-25.2% SL (23.4%); head length 29.5-33.2% SL (31.2%); snout length 21.6-28.7% HL (27.3%); orbit diameter 21.1-29.3% HL (21.1%); interorbital space convex, width 25.8-33.6% HL (33.6%); preorbital depth 22.2-27.3% HL (27.3%).

Mouth small, slightly inferior, maxilla reaching a vertical from just beyond anterior margin to nearly the anterior third of eye, upper-jaw length 25.6-35.5% HL (35.5%); numerous rows of small slightly curved conical teeth at front of jaws, narrowing to a single row posteriorly, outer row slightly enlarged and somewhat movable; lips fleshy; chin with 3 pairs of prominent pores.

Scales small and ctenoid; lateral line gently curved, following dorsal contour of body; head scaled except snout just forward of anterior nostrils (to anterior nostrils in holotype), and a naked band to eye; small scales basally on median fins, those on dorsal extending about 1/4 distance to margin; opercle with a single flat blunt spine; margin of preopercle very finely serrate, serrae slightly larger at corner.

Dorsal fin scarcely notched, interspinous membranes not incised; base of spinous portion of dorsal fin 26.9-31.2% SL (27.8%); base of soft portion of dorsal fin 36.6-41.1% SL (36.6%); first dorsal spine about half length of second, 43.2-60.4% (49.3%); longest dorsal spine the third or fourth, 34.0-55.9% HL (third, 34.0%); longest dorsal soft ray 44.5-61.5% HL (44.5%); base of anal fin 28.9-35.7% HL (28.9%); first anal spine very short, 7.0-12.9% HL (7.0%); second anal spine 25.8-45.1% HL (25.8%); third anal spine 28.1-45.4% HL (28.1%); longest anal ray 53.1-69.6% HL (53.1%), reaching when adpressed more than half distance to caudal-fin base; caudal fin truncate to slightly emarginate, its length 20.0-23.8% SL (20.7%); longest pectoral ray 21.1-21.9% SL (21.5%); pelvic fins reaching to or slightly beyond vent, 24.1-27.4% SL (24.1%).

Colour in alcohol of holotype: light brown with numerous small dark brown spots on head, dorsally on body, dorsal fin, and upper 3/4 of

TABLE 1. Proportional measurements of the type specimens of *Diagramma melanacrum* expressed as a percentage of standard length.

	Holotype	Paratypes			
	QMI20291	QMI30725	QMI20285	BPBM 26719	BPBM 26719
Standard length (mm)	410.0	187.0	133.0	219.0	254.0
Body depth	41.5	38.0	38.7	40.4	41.3
Body width	16.3	15.5	12.8	12.8	14.4
Head length	31.2	33.2	30.8	29.5	31.7
Snout length	8.5	9.5	7.9	6.4	8.3
Upper jaw length	11.1	9.4	7.9	9.0	9.4
Orbit diameter	6.6	8.0	9.0	8.2	7.9
Preorbital depth	8.5	7.5	6.8	6.8	7.7
Interorbital width	10.5	8.6	8.4	9.2	9.8
Caudal peduncle depth	10.7	11.4	11.8	11.7	11.7
Caudal peduncle length	23.4	22.6	25.2	24.0	23.4
Spinous dorsal base	27.8	29.4	29.3	31.2	26.9
Soft dorsal base	36.6	36.7	36.6	38.8	41.1
First dorsal spine	4.3	7.5	10.2	6.1	6.0
Second dorsal spine	8.7	15.2	16.9	13.9	13.7
Third dorsal spine	10.6	16.7	16.8	14.3	14.7
Fourth dorsal spine	10.0	16.8	17.2	13.6	14.2
Fifth dorsal spine	9.9	15.8	15.6	13.0	13.4
Longest dorsal ray	13.9	20.3	15.8	18.2	16.1
Anal fin base	9.0	11.2	10.9	10.5	10.9
First anal spine	2.2	4.3	4.0	3.3	2.5
Second anal spine	8.0	13.0	13.9	12.1	11.6
Third anal spine	8.8	14.2	14.0	12.8	12.6
Longest anal ray	16.6	20.9	19.5	20.5	19.7
Caudal fin length	20.7	23.8	23.3	21.5	20.0
Longest pectoral ray	21.5	21.9	21.1	21.8	21.7
Longest pelvic ray	24.1	27.4	25.9	25.3	25.1

caudal fin; spots below lateral-line smaller, not as dark, very close-set, following centres of oblique scale rows; spots on snout and interorbital smaller and more close set than those on remainder of head and upper body; opercular membrane dark brown; lower 1/4 of caudal fin and all but basal part of anal and pelvic fins dark brown; pectoral fins dusky, the upper half of base with a dark brown bar that curves over dorsal edge of fin base to axilla. Paratypes, 133-254mm SL: Similar to holotype except spots on head, body and caudal fins progressively smaller and greater in number with increasing size. Operculum and cheeks with narrow discontinuous wavy longitudinal lines extending to about level of anterior of eye. Anteriorly, on snout, lines replaced by small dark brown spots as in holotype.

Colour in life from underwater photographs

(specimens not collected): snout, interorbital, nape, body mostly above lateral-line, dorsal fin, and upper 3/4 of caudal fin pale yellow with numerous small dark brown spots; body below lateral-line light grey with numerous faint close-set orange brown spots, smaller than those dorsally on body, and arranged in oblique rows; head light purplish grey with numerous small dark orange brown spots; ventral part of head and body whitish; opercular membrane black; lower 1/4 of caudal fin black; anal and pelvic fins whitish basally, soon shading to black distally, the leading edge of pelvics narrowly whitish; pectoral fins pale with dusky rays and a narrow dark reddish brown bar at base. Subadults of about 250mm TL with narrow discontinuous wavy longitudinal dark brown lines on head, extending from about anterior margin of eye to opercles. The colour pattern of small juveniles is unknown.

REMARKS. Kuiter (1993; 1996), Kuiter & Debelius (1994) and Eichler & Myers (1997) recognised 2 species of *Diagramma*, *D. pictum*

(Thunberg), widespread in the Indo-west Pacific excluding Australia and S PNG, and *D. labiosum* Macleay from Australia and S PNG. Sightings of both species from Flores, Indonesia were reported by Rudie H. Kuiter (pers. comm., 1996), but the presence of *D. 'labiosum'* in this area has not been substantiated by specimens or photographs. J. Barry Hutchins reported (pers. comm., 2000) that *D. 'labiosum'* was absent from Ashmore Reef. This is not surprising as the fish fauna of this reef has close affinities to Indonesia and includes species typically Indo-Malaysian, some of which are not known from Australian inshore waters (Allen, 1993). Another haemulid, *Plectorhinchus vittatus* (Linnaeus) is recorded from offshore reefs at Ashmore, Hibernia and Rowley Shoals, but not from other Australian waters.

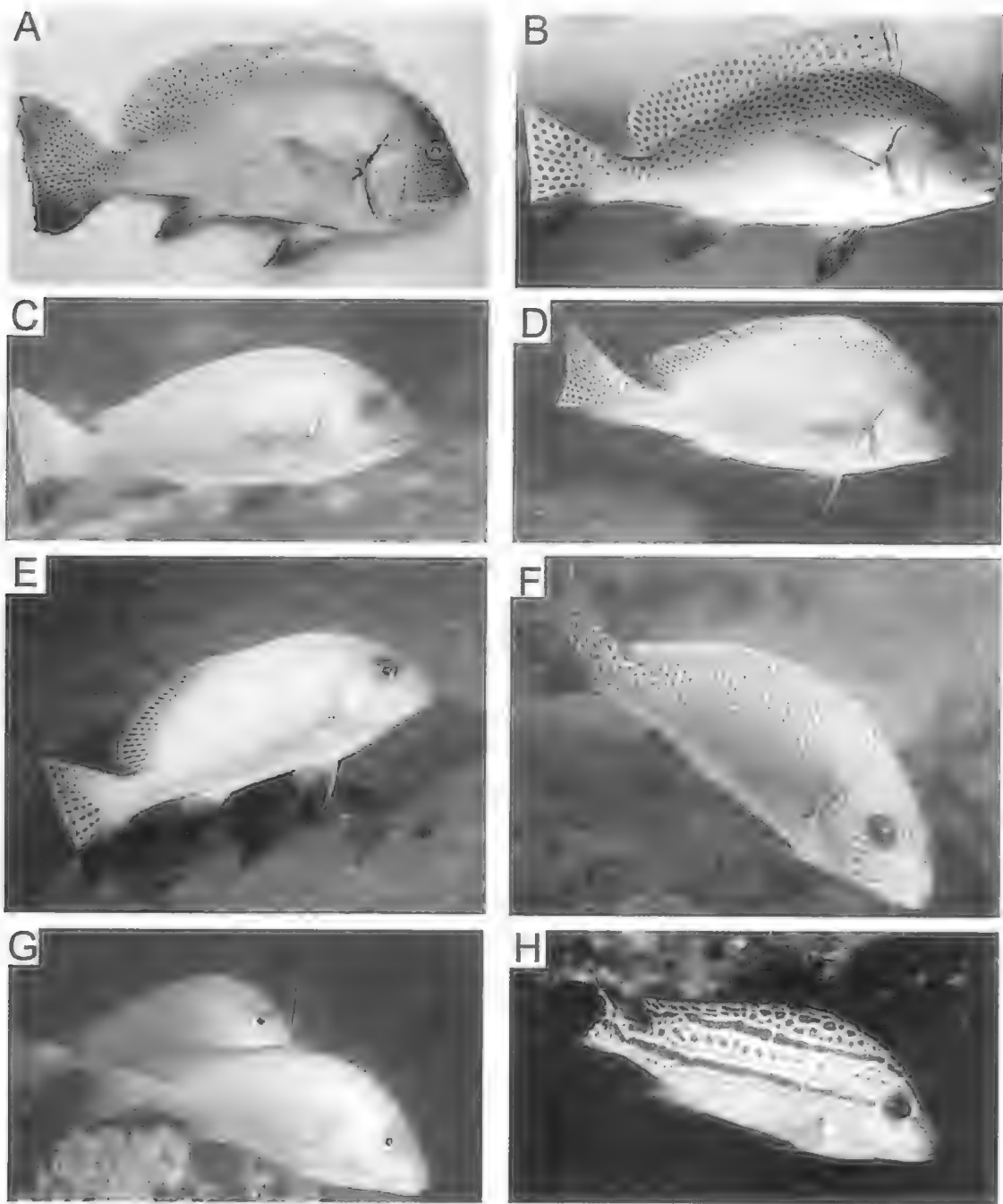


FIG. 1. A, *Diagramma melanacrum* Holotype, QM I.20291, 410mm SL, Lombok, Indonesia, T. Gloerfelt-Tarp. B, *Diagramma melanacrum* Paratype, BPBM 26719, 254mm SL, Off Ujung Pandang, Sulawesi, J.E. Randall. C, *Diagramma melanacrum* ~350mm TL, Romang Island, Indonesia, J.E. Randall. D, *Diagramma melanacrum* ~330mm TL, Moyo Island, Indonesia, J.E. Randall. E, *Diagramma melanacrum* ~350mm TL, Tomini Bay, Sulawesi, R.H. Kuiter. F, *Diagramma melanacrum* ~250mm TL, Mabul, Borneo, R.H. Kuiter. G, *Diagramma pictum labiosum*, 300mm TL, Lizard Is., Australia, J.E. Randall. H, *Diagramma pictum labiosum*, ~130mm TL, Sydney Harbour, Australia, R.H. Kuiter.

TABLE 2. Meristic data of *Diagramma* species.

	Tubed Lateral-line Scales																							
	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78
<i>melanacrum</i>	2	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>pictum labiosum</i>	-	-	-	-	2	1	-	1	1	1	1	4	7	6	7	10	3	2	4	4	2	4	-	1
<i>pictum pictum</i>	-	-	4	3	5	5	3	1	1	5	9	4	2	5	2	3	2	1	-	2	-	-	-	-
<i>pictum cinerascens</i>	1	5	1	7	3	2	1	2	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>pictum centurio</i>	-	2	1	3	8	1	1	2	2	3	-	1	-	-	-	-	-	-	-	-	-	-	-	-
<i>pictum punctatum</i>	2	1	1	2	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

	Gill Rakers														Total								
	Upper					Lower																	
	5	6	7	8	9	11	12	13	14	15	16	17	17	18	19	20	21	22	23				
<i>melanacrum</i>	-	4	1	-	-	-	-	4	1	-	-	-	-	-	3	2	-	-	-				
<i>pictum labiosum</i>	3	33	22	3	-	-	1	19	37	4	-	-	-	1	14	26	16	3	1				
<i>pictum pictum</i>	1	18	26	7	1	-	-	9	36	6	1	1	-	-	6	14	21	6	5				
<i>pictum cinerascens</i>	-	6	15	3	-	1	5	11	7	-	-	-	1	1	6	8	8	-	-				
<i>pictum centurio</i>	-	1	9	16	2	-	-	-	12	16	-	-	-	-	-	-	6	9	13				
<i>pictum punctatum</i>	-	-	6	2	-	-	-	2	3	3	-	-	-	-	-	2	3	1	2				

	Dorsal Spines			Dorsal Rays								Pectoral Rays		
	IX	X	XI	20	21	22	23	24	25	26		16	17	18
<i>melanacrum</i>	2	3	-	-	-	1	-	4	-	-		-	5	-
<i>pictum labiosum</i>	12	50	-	-	-	3	16	29	12	2		3	16	13
<i>pictum pictum</i>	13	43	-	1	6	17	13	14	5	-		2	48	6
<i>pictum cinerascens</i>	2	21	1	-	3	11	8	2	-	-		-	20	4
<i>pictum centurio</i>	7	22	-	-	1	5	11	10	2	-		-	25	3
<i>pictum punctatum</i>	-	8	-	-	-	2	4	2	-	-		-	5	3

Diagramma pictum and *D. 'labiosum'* are distinguished on few characters other than colouration, with all meristic and morphometric values strongly overlapping (Tables 2, 3). Small juveniles are difficult if not impossible to separate. Given the similarity between *pictum* and *'labiosum'* there was some doubt as to whether they should be separated at the specific or subspecific level (as geographically separate colour forms). With no firm evidence of sympatry, which would lend support to the premise of separate species status, it was decided that some tests would be conducted to determine the genetic variability among and between Australian and SE Asian populations, and to see if these indicated more conclusive separation.

DNA ANALYSIS. Fresh frozen specimens of *D. 'labiosum'* were obtained from the following widely separated Australian localities: 1) Comboyuro Point, Moreton Bay, Qld (4 fish); 2) North West Island, Capricorn Group, Qld (4 fish); 3) Gulf of Carpentaria, Qld (3 fish); 4) off Port Headland, WA (3 fish). Specimens of *D. pictum* were obtained from Senoko Fishery Port, Singapore (4 fish). One specimen of

Plectorhinchus flavomaculatus (Ehrenberg, 1830) from off Mackay, Queensland, Australia was used to gain an outgroup sample. Frozen muscle tissue from the lower caudal peduncle was removed from each specimen for analysis.

TABLE 3. Selected morphometric data of *Diagramma melanacrum*, *D. pictum pictum* and *D. pictum labiosum*.

	<i>D. melanacrum</i>	<i>D. p. pictum</i>	<i>D. p. labiosum</i>
Number of specimens	5	33	40
Standard length (mm)	133-410	130-503	129-620
Percentage of standard length			
Depth	38.0-41.5	35.8-40.6	31.3-41.3
Head length (HL)	29.5-33.2	26.8-31.5	25.7-32.6
Orbit diameter	6.6-9.0	5.4-9.5	4.5-8.7
Caudal peduncle length (CPL)	22.6-25.2	22.9-27.9	24.2-28.9
Caudal peduncle depth (CPD)	10.7-11.8	9.6-11.9	8.7-12.3
Pelvic fin length	24.1-27.4	18.7-23.8	17.0-24.3
Ratio CPL:HL	1.2-1.5	1.0-1.3	0.9-1.3
Ratio CPD:CPL	2.0-2.2	2.0-2.8	2.2-3.1

TABLE 4. Cytochrome B nucleotide diversity within (bold) and among pairs of samples of *D. pictum* (5) and *D. 'labiosum'* (1-4).

		1	2	3	4	5
1	Moreton Bay (n = 4)	0.000	0.000	0.003	0.002	0.005
2	North West I. (n = 4)	0.000	0.000	0.003	0.002	0.005
3	Gulf of Carpentaria (n = 3)	0.005	0.005	0.003	0.001	0.003
4	North West Shelf (n = 3)	0.005	0.005	0.006	0.006	-0.001
5	Singapore (n = 4)	0.005	0.005	0.005	0.003	0.000

Our aim with the mitochondrial DNA analysis was to determine if each of the *D. 'labiosum'* and *D. pictum* forms formed monophyletic mtDNA clades. Such a pattern would have allowed us to conclude that the 2 colour forms have existed allopatrically for a considerable amount of time (at least 4N generations (Avise et al., 1984)) and may have provided an insight to the 2 forms being separate species. The results are however inconclusive as mtDNA haplotypes do not cluster by colour form or location (Tables 4, 5). That haplotype 4 is shared between forms in the North west Shelf and Singapore provides evidence of gene flow between the 2 forms (Fig. 2). It should be noted however that several Indo-Pacific species of butterflyfishes *Chaetodon* are paraphyletic for Cytochrome B sequences despite being considered good species (McMillan & Palumbi, 1995). This may reflect the rapid diversification of the *Chaetodon* species complex and suggests that there has not been sufficient time since speciation for complete mtDNA lineage sorting. Such a situation cannot be rejected for *D. 'labiosum'* and *D. pictum* on the basis of our cytochrome B data set.

Thus mitochondrial DNA analysis alone does not provide a perfect test of species status due to its haploid non-recombining nature (Avise, 1994). An assay of nuclear genes from areas where the two forms are sympatric would have provided a more powerful test of the taxonomic status of the two forms. This luxury was not afforded in the present study for two reasons. First, reports of the two forms existing in sympatry are anecdotal at best. The one report from southern Indonesia is based only on sightings of large adults, in which colour is a less reliable distinguishing feature. No specimens of *D. 'labiosum'* from this region have been located. Despite extensive collecting efforts off northern

TABLE 5. Cytochrome B haplotype frequencies for samples of *D. pictum* and *D. 'labiosum'*.

Location	Haplotype Frequencies				
	1	2	3	4	5
Moreton Bay	4	-	-	-	-
North West Is.	4	-	-	-	-
Gulf of Carpentaria	-	2	1	-	-
North West Shelf	-	1	-	1	1
Singapore	-	-	-	4	-

Australia, no specimens of the *D. pictum* form have been found. Second, tissue material could not be transported back to the laboratory from SE Asian sites in good enough condition to permit allozyme electrophoresis to be carried out.

On this basis, and results enunciated below, it was decided that the separate colour forms be recognised as subspecies of *D. pictum* Thunberg.

Diagramma pictum pictum (Thunberg, 1792)
(Common name: Yellow-spotted Slatey)
(Figs 3A-H, 8)

Perca picta Thunberg, 1792 (Japan).

Perca pertusa Thunberg, 1793 (Japan).

Holocentrus radjahan Lacepède, 1802 (East Indies).

Diagramma baiteatum Cuvier, 1830 (Java).

REMARKS. *D. pictum pictum* is known from the W Pacific and Indo-Malay Archipelago, N to Japan and S to New Caledonia, but excluding Australia and S New Guinea. Various stages are figured in colour, from Japan (Burgess & Axelrod, 1972, pls 392-393; Masuda et al., 1984; Masuda & Kobayashi, 1994:162, pls 1-3, 5-6 (note fish in pl. 4 are *D. pictum labiosum* from the Great Barrier Reef, Australia); Okamura et al., 1997: 352, 12 pls of specimens 2.5 to 65cm; Masuda, 2000: 96), through Taiwan (Shen, 1984:

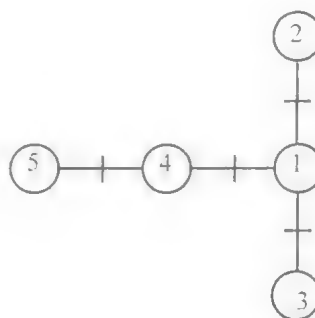


FIG. 2. Minimum spanning network of the relationships among Cytochrome B sequences. Each dash represents a single nucleotide substitution.

pl. 65 no. 327-6a,b,c, pl. 66 no. 327-8b&c; Burgess & Axelrod, 1974: pls 271, 275-276), the Philippines (JER photo QM NR63), Palau (Myers, 1999, pl. 67, a&b), Indonesia (Gloerfelt-Tarp & Kailola, 1984; Kuiter & Debelius, 1994; photos JER (QM NR62) and R.H. Kuiter (QM NR52)), Rabaul, New Britain (Allen & Steene, 1987, pls 50-8), New Caledonia (Fourmanoir & Laboute, 1976: 99; JER photo QM NX793-795) and Santo, Vanuatu (Burgess & Axelrod, 1975, pl. 222-223). Fowler (1931) illustrated in black and white a range of 12 juvenile colour variations, one of which (fig. 22, lower left) is similar to a juvenile paratype of *D. melanacrum* (QMI20284), but lacks the width and intensity of black pigmentation to the lower caudal lobe.

D. pictum pictum is distinguished by relatively large, close-set, yellow to burnt orange spots on head, body and unpaired fins in juveniles from about 160mm TL, subadults, and at least smaller adults. This subspecies progresses from the striped to fully spotted phase at 160-200mm TL. Diameter of the spots varies from about 1-3 times in the pupil or 2-5.3 times in the eye diameter. Short bars and wavy lines of the same colour are often present, mostly on the suborbital and operculum, in specimens larger than 160mm TL, but usually break up into spots in large specimens. Specimens to about 600mm TL usually retain conspicuous, although relatively smaller, spots on the body and particularly the cheeks. In fish above 800mm TL, spots on the body have often faded into a generally plain slate or silver-grey ground colouration, but there are usually at least some yellowish spots remaining on the lower head. We have no records of specimens with scattered dusky blotches, as is common in other large *D. pictum* subspecies. This subspecies also lacks the rows of bronze centres to individual scales present in *D. pictum punctatum*. The only other subspecies to share yellowish spots, or yellow pigmentation on the unpaired fins of all but small juveniles, is *D. pictum cinerascens*. However, in the latter the spots fade and disappear from the body at a much earlier stage, at about 300 to 400mm TL. Other subspecies have darker, usually brownish spots. The median tubed lateral-line scale count of 65 (range 57-74) is lower than the median of 69 recorded for *D. pictum labiosum* (range 59-78), but is higher than that for all other *pictum* subspecies (median 58-59, range 55-66). The median dorsal ray count (23) is lower than for *D. pictum labiosum* (24), but higher than that of *D.*

pictum cinerascens (22). The median total gill raker count (21) is higher than that for *D. pictum labiosum* and *D. pictum cinerascens* (20) and lower than that for *D. pictum centurio* (22).

***Diagramma pictum labiosum* Macleay**
(Common name: Australian Slatey)
(Figs 1G-H, 4A-H, 8)

Diagramma labiosum Macleay, 1883 (Wide Bay, Queensland).

REMARKS. *D. pictum labiosum* is known from S New Guinea and N Australia, from Houtman Abrolhos, WA, E to Lord Howe Island and Sydney, NSW. It is figured in Burgess & Axelrod (1976: pls 345 & 350-354), Coleman (1980: 160), Grant (1982: pl. 190; 1987: pl. 456), Sainsbury et al. (1985: 215), Allen & Steene (1987: pls 51-2), Randall et al. (1990 & 1997: 191), Kuiter (1993, 1996) and Masuda & Kobayashi (1994: 162, pl. 4).

Macleay (1883) described *D. labiosum* from a single 300mm specimen. The type is no longer extant (Eschmeyer, 1998). Macleay made reference to dense spotting on the soft dorsal and caudal fins, but not to any spots on the head and body. He stated that 'the general colour is a dark silvery bluish grey'. This is consistent with fresh specimens from Australian waters, some of which had lost all spots on the head and body by 250mm TL, and all by 300-350mm TL. It is usual for other subspecies, except for *D. pictum centurio* from E Africa, to exhibit spots at 300mm.

D. pictum labiosum has relatively small, close-set dark brown to bronze spots on the head and body in specimens from about 150-300mm TL. These spots vary in diameter from 2.6-6.5 times in pupil or 4.7-11.6 times in eye, rapidly diminishing in size on fish from 150-200mm TL. The stripes of the juvenile stage break up into a larger number of much finer spots than in any other subspecies. Golden-brown to dusky spots and short bars may be present on the suborbital and operculum of juveniles, but fade and disappear by about 200mm TL. Small dark brown spots gradually fade and disappear from the anterior toward the posterior part of the body with age. From 200-300mm TL spots on the body have reduced to a cluster of spots less than 1/4 pupil diameter, peppered on the upper half of the caudal peduncle. Beyond 350mm TL, all spots have disappeared and the head and body are plain slate to sooty silver-grey, often with some violet reflections on the cheeks. Adults, especially those in excess of 500mm TL, often develop scattered diffuse dusky blotches. In most

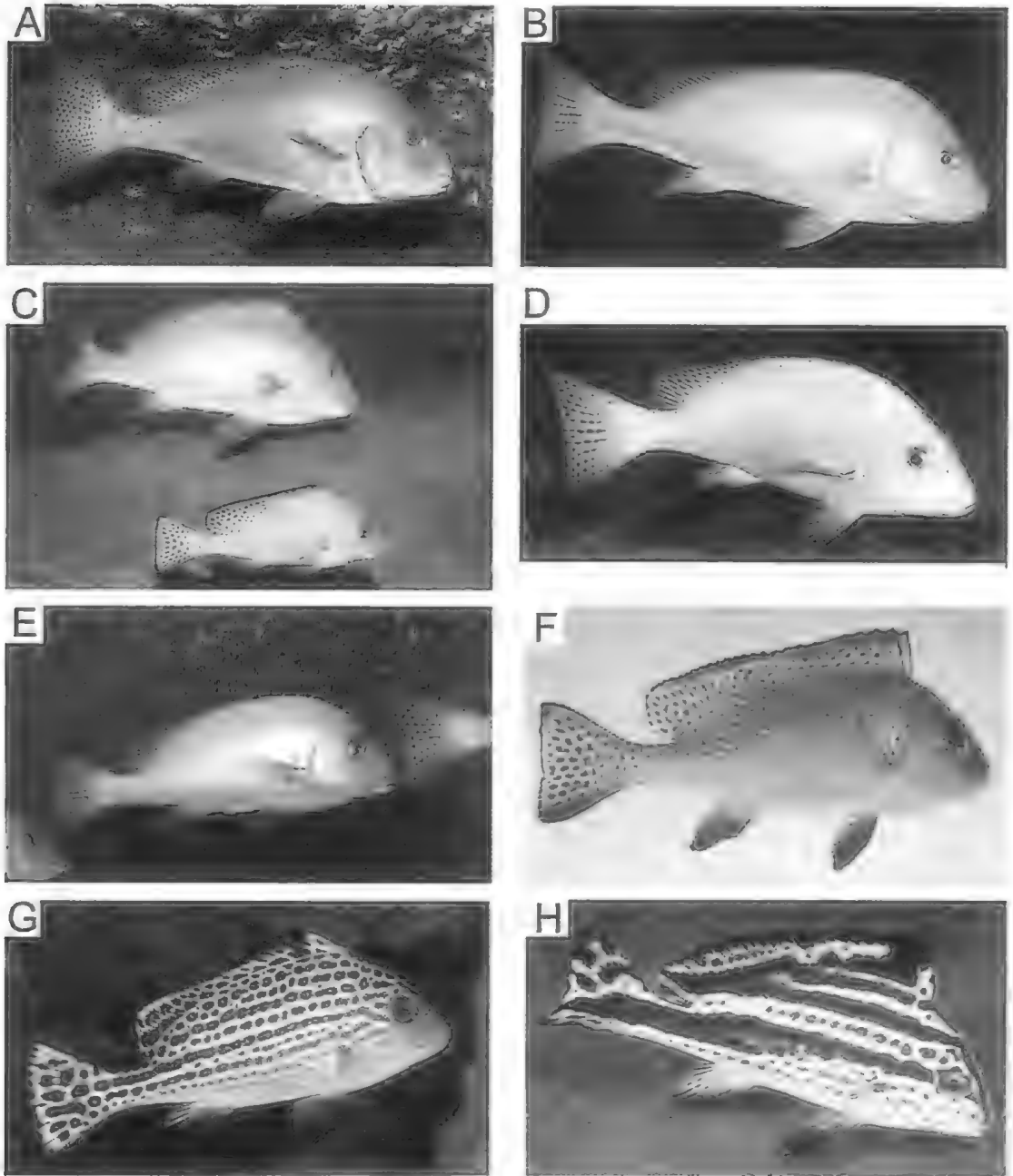


FIG. 3. *Diagramma pictum pictum*; A, ~800mm TL, Maumere, Flores, R.H. Kuiter; B, 800mm TL, Menjangan Is., Bali, R.H. Kuiter; C, ~550mm TL and ~250mm, Flores, Indonesia, R.H. Kuiter; D, ~350mm TL, Tomini Bay, Sulawesi, R.H. Kuiter; E, ~300mm TL, New Caledonia, J.E. Randall; F, 236mm TL, Dumaguete, Philippines, J.E. Randall; G, ~200mm TL, Amed, Bali, R.H. Kuiter; H, ~150mm TL, Bitung, Sulawesi, R.H. Kuiter.

individuals numerous small spots persist on the caudal and rear of the soft dorsal fin, even in specimens of 1000mm TL. At all comparable

sizes, spots on these fins are greater in number and smaller in diameter than in *D. pictum pictum*. In specimens 350-500mm TL, a maximum of

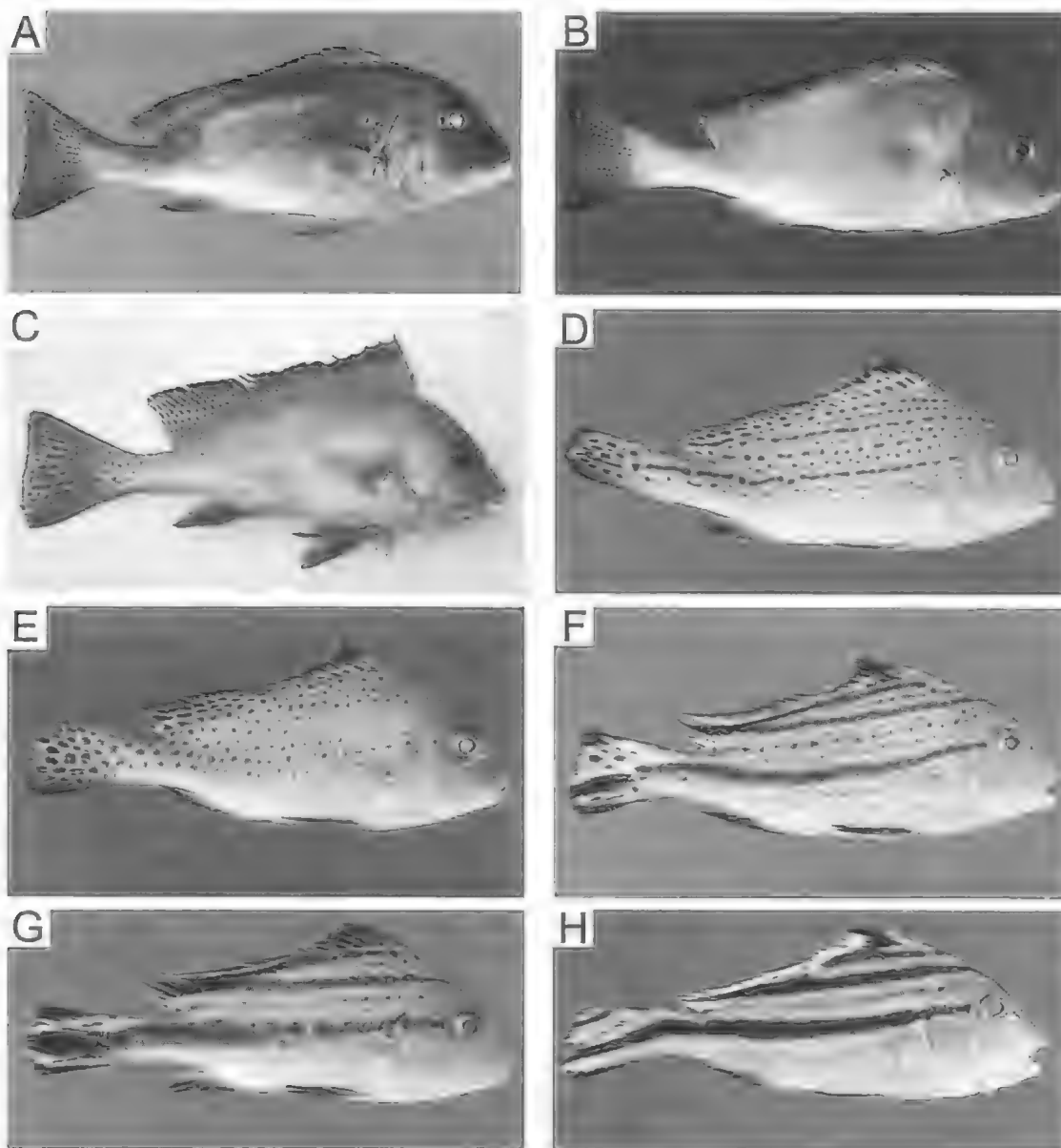


FIG. 4. *Diagramma pictum labiosum*; A, 392mm TL, Moreton Bay, Australia, J.W. Johnson; B, 335mm TL, North West Is., Great Barrier Reef, Australia, J.W. Johnson; C, ~220mm TL, Shark Bay, Western Australia, R.J. McKay; D, 160mm TL, Gulf of Carpentaria, Australia, J.W. Johnson; E, 146mm TL, Gulf of Carpentaria, Australia J.W. Johnson; F, 136mm TL, Gulf of Carpentaria, Australia, J.W. Johnson; G, 126mm TL, Gulf of Carpentaria, Australia, J.W. Johnson; H, 108mm TL, Gulf of Carpentaria, Australia, J.W. Johnson.

9-14 rows of spots on the soft dorsal fin membrane and 12-20 rows of spots on the caudal fin membrane parallel to the fin rays were recorded, versus a maximum of 4-6 and 6-10 respectively for *D. pictum pictum*. This species lacks yellow or orange spots at any size and has

no bars or wavy lines on the head, except occasionally in small juveniles. Adults have a scarlet to crimson-red throat, from the rear of the palate to the interior of the operculum and branchiostegal membranes, as well as the outer

gill arch membranes, broadly in common with other subspecies.

D. pictum labiosum progresses from a striped to a fully spotted stage at a smaller size than other subspecies of *Diagramma* (130–160mm TL); and spots, while present, are smaller and more close-set at any given size than other subspecies. Subadults lose all markings on head and body at a smaller size (300–350mm TL) than all other subspecies, except some *D. pictum centurio* from E Africa. It differs from other subspecies by a higher median lateral-line scale count (69 versus 57–65) and, more importantly, the upper range of lateral line scale counts in all other *Diagramma* (except *D. pictum pictum* with 74), is below the median for *D. pictum labiosum*. The median total gill raker count (20) is lower than for all other *D. pictum* subspecies (21 or 22), except *D. pictum cinerascens*; and the median soft dorsal ray count (24) is higher than all other *D. pictum* subspecies (22 or 23).

***Diagramma pictum cinerascens* Cuvier**
(Common name: Fork-striped Slatey)
(Figs 5A–H, 8)

Diagramma cinerascens Cuvier, 1830 (Trincomalee, Sri Lanka).

Diagramma blochii Cuvier, 1830 (Trincomalee, Sri Lanka).

Diagramma poecilopterus Cuvier, 1830 (Pondicherry, India).

REMARKS. *Diagramma pictum cinerascens* occurs in the Indian Ocean from the Bay of Bengal to the Persian Gulf. It is figured in colour photographs taken by R.H. Kuiter (QM NR48–49), Kuiter (1998:104), JER (QM NL742) and H. Voigtmann (in Debelius, 1999: 100, top left) from the Maldives; from Sri Lanka (Debelius, 1999: 100); from the Persian Gulf by Randall (1992, pl. 130a) and J. Hoover (in Randall, 1995, pls 528–530) and from the Gulf of Oman by P. Woodhead (in: Debelius, 1993: 127 top left, p. 128 centre, and Debelius, 1998: 88 centre) from Ras al Hamra, Oman.

The brief original description of *D. cinerascens* is from a 256mm SL specimen, MNHN 7803 (Bauchot et al., 1983). The holotype has a uniform brown body and small darker brown spots on the rays of the dorsal and anal fins. Cuvier (1830) gave a dorsal ray count of 'XII/16?' for *D. blochii*, which suggests a species of *Plectorhinchus*, however his description was based on a drawing by Raynaud and the query given after the count suggests he had difficulty in discerning the true fin formula from the drawing. His dorsal, anal and pectoral

fin formulae for *D. poecilopterus* are also shown to be erroneous by Smith (1962). Smith examined the holotype and paratype (MNHN 7811 from Pondicherry and 7810 from Trincomalee, respectively) and obtained counts consistent for this form (Table 2). Stripes on the 155mm SL holotype, as depicted in Smith (1962: fig. 22), are usual for specimens of this size.

This subspecies differs from others in the configuration of the body stripes of juveniles, the size of the spots, and nature of the lines on the cheeks and operculum of large juveniles to small adults. Juveniles progress from a striped to a fully spotted phase at 180–240mm TL. Juveniles of about 150mm TL often have broad, clearly defined body stripes, not yet beginning to break into broken lines or numerous spots, as is usual for other *Diagramma* of this size. As mentioned by Day (1878), unlike juvenile stages of any other form of *Diagramma*, the second and third stripes on the body merge to form a single stripe above the posterior half of the pectoral fin (Day, 1878, pl. 21, fig. 3; Debelius, 1993, fig. p. 127; Randall, 1992, pl. 130a; Smith, 1962, fig. 22). At the point where the stripes merge, there is often a small break or up-curved interruption in the stripe. The front of the head, including the snout to the interorbital and suborbital, as well as much of the dorsal and caudal fin membrane, may be bright yellow in fish of up to about 200mm TL. In specimens from about 200–350mm TL, there are usually wavy yellowish lines or spots on the operculum and cheeks. The lines are narrow in larger specimens, but vary in width in small specimens. Spots on the body are tan to orange-brown, in longitudinal rows. In specimens about 180–300mm TL, the spots range from 3.1–6 in eye diameter. The spots are generally smaller and more close-set than *D. pictum pictum*, larger and more close-set than *D. pictum centurio* and larger and more sparse than in *D. pictum labiosum*. Unlike the latter, they do not fade and disappear first from the dorso-anterior region, producing a life-stage with a cluster of spots on the upper part of the caudal peduncle only. The only other subspecies to have lines or bars on the head of specimens above 180mm TL is *D. pictum pictum*, however, in the latter, these are usually broader and accompanied by yellow or orange spots on the body. Specimens in excess of 400mm TL are generally plain slate to silver-grey, often with scattered irregular dusky blotches on the head and body, similar to large *D. pictum labiosum*. However, unlike the latter, narrow wavy yellowish lines or small spots may still be evident

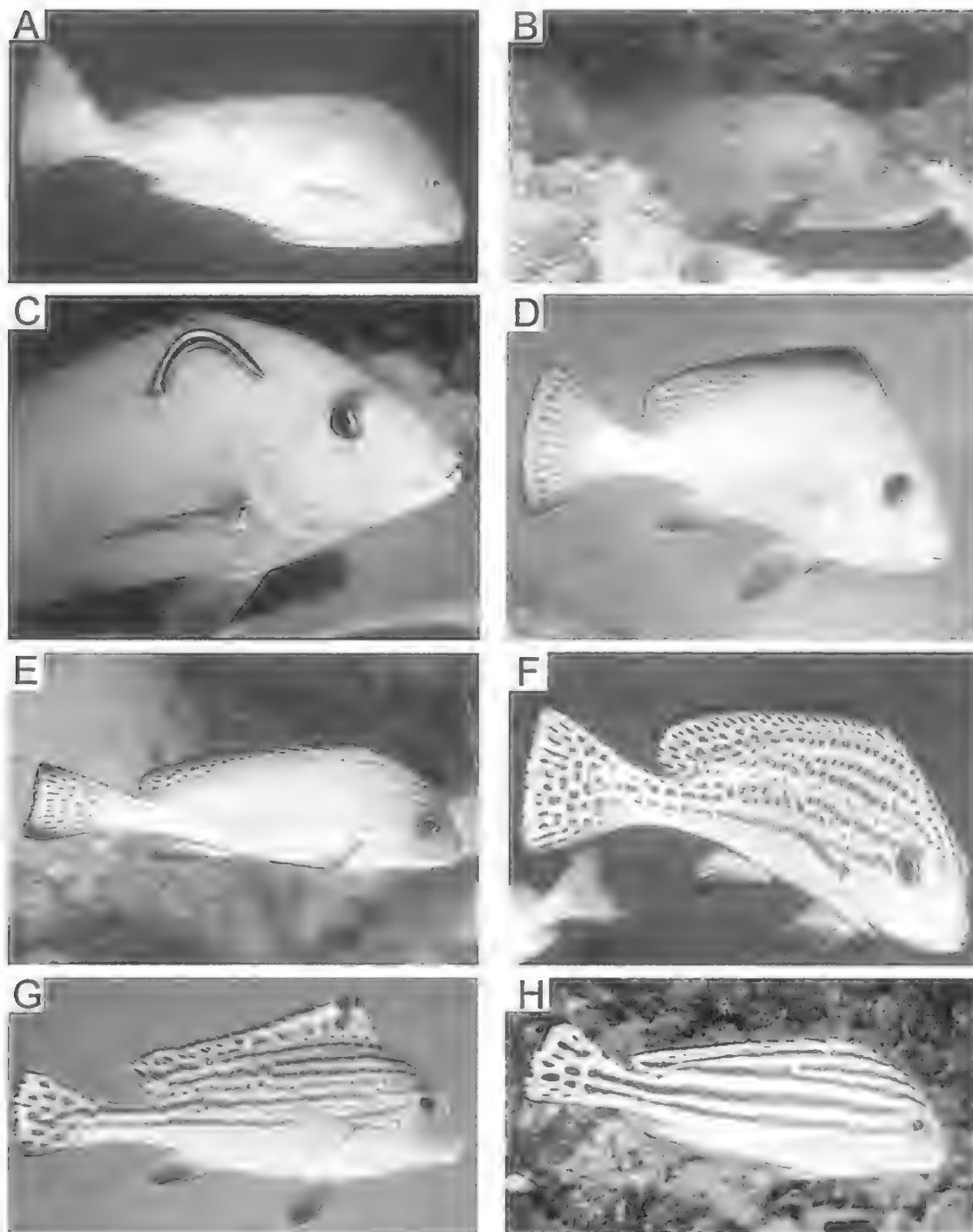


FIG. 5. *Diagramma pictum cinerascens*; A, ~800mm TL, Oman, J.P. Hoover; B, ~500mm TL, Great Basses, Sri Lanka, R.C. Anderson; C, ~450mm TL, Maldives, R.H. Kuiter; D, ~300mm TL, Oman, J.P. Hoover; E, ~240mm TL, Trincomalee, Sri Lanka, R.C. Anderson; F, ~200mm TL, Trincomalee, Sri Lanka, R.C. Anderson; G, 172mm TL, off Bahrain, Persian Gulf, J.E. Randall; H, ~150mm TL, Oman, P. Woodhead.

from the suborbital to the rear of the operculum in some larger specimens. This subspecies is best distinguished by the unique striped pattern of the juvenile and by the narrow yellowish wavy lines or spots on the head in small adults. It has a lower median lateral line scale count (58) than *D. pictum pictum* (65) and *D. pictum labiosum* (69); fewer median total gill rakers (20) than other *D. pictum* subspecies (21 or 22), except *D. pictum labiosum*; and fewer median dorsal fin rays (22) than all other subspecies (23 or 24).

***Diagramma pictum punctatum* Cuvier**
(Common name: Red Sea Slatey)
(Figs 6A-H, 8)

Diagramma punctatum Cuvier, 1830 (Red Sea).

Diagramma punctatum Rüppell, 1830 (Northern Red Sea).

Diagramma cinerascens (non Cuvier) Rüppell, 1830 (Red Sea) - name preoccupied by *D. cinerascens* Cuvier.

REMARKS. *Diagramma pictum punctatum* is known only from the Red Sea. It is figured in colour photographs by GR. Allen at Jeddah (QMNR54-55); JER at Sudan and Nuweiba, Egypt (McKay, in Fischer & Bianchi, 1984: vol. II, pl. 2; Randall, 1983: pl. 111; Randall, 1992: pl. 130b); JER photos at Gulf of Aqaba (QMNX806) and Dahab, Egypt (QMNX807); R. Kuitert photo at Egypt (QMNX800); D. Eichler photo (QMNX798) and H. Debelius photos at Sinai, Egypt (Debelius, 1998: 88 upper left (adult) and upper right (large juvenile)), QMNX799.

Cuvier (1830) in his account of *D. punctatum*, initially referred to 3 specimens collected by Ehrenberg. A description and meristic formulae for this material was quoted separately and a single specimen 9 inches in length was listed. These specimens were from the Red Sea and are represented by one unregistered specimen in the Natural History Museum, Humboldt University, Berlin (Eschmeyer, 1998). Cuvier went on to mention other material of *Diagramma* sourced by Kuhl and van Hasselt from Java (RMNH D 2172); Stadhouder from the Indian Archipelago (MNHN 7836 (1), MNHN A.7832 - latter specimen is the holotype of *D. radjabau* Lacépède, 1802); Raynaud from Batavia (MNHN 7801 (1)); and Quoy & Gaimard from Vanicolo (MNHN 7802 (2)). The museum catalog numbers for these specimens were listed by Bauchot et al. (1983) and Eschmeyer (1998). Cuvier recognised all the material from the East Indies as *D. radjabau* of Lacépède (1802), and surmised that the Ehrenberg material from the Red Sea was 'the same species, or very near' to it. However, Cuvier's description of *D. punctatum* was not a compilation of the Red Sea and East Indian forms of *Diagramma*. The Ehrenberg material was treated separately in the initial

stages of the paper, followed by an account of other specimens from the east, including a redescription of the type material of *Holocentrus radjabau*. Also, Cuvier, by his equivocal comments above, cast doubt on whether the other specimens were conspecific with the Red Sea material. The unregistered ZMB specimen from the Ehrenberg collection is implicitly the holotype and the rest constitute other material, rather than part of a syntypic series. Rüppell (1830) also proposed *D. punctatum* for specimens from the N Red Sea, catalogued SMF 2215 (2), but appears to have been pre-empted by Cuvier (Eschmeyer, 1998).

D. pictum punctatum has dark brown, orange-brown to golden tan spots on the head and body of most specimens in excess of 140mm TL. In smaller specimens the spots are usually slightly elongate, and individual spots along the rows may be slightly inclined obliquely. Juveniles transform at about 135-145mm TL from a colour pattern including 3 broad dark stripes, to a phase that is uniformly marked with spots of approximately equal size. The spots on the body of large juveniles and subadults (180-350mm TL) are smaller than in *D. pictum pictum*, similar to *D. pictum cinerascens*, but larger than other *Diagramma* subspecies. They are fewer than in *D. pictum labiosum* and usually greater than in *D. pictum centurio*. From about 140-350mm TL spots generally decrease from about 1/2 to 1/4 pupil diameter, or 4.1-6.6 in eye diameter. At this size, there is no bright yellow pigmentation to the head, body or fin membranes, as in some *D. pictum cinerascens* and *D. pictum pictum*. The ground colour of adults is plain silver-grey to grey-bronze. Adults usually have small round dark brown spots on the upper head and along the upper body to the caudal peduncle, above the lateral-line. The only other subspecies to have distinct spots on the body in adults is *D. pictum pictum*, however in the latter the spots (when present) are larger, usually lighter in colour and not confined to the upper margin of the body. In adults there are bronze centres to individual scales, forming rows, a feature absent or very ill-defined in other forms. Few specimens were available for examination; however the lateral-line scale counts obtained (55-61) are at the low end of the range for the genus and modally well below that for *D. pictum labiosum*.

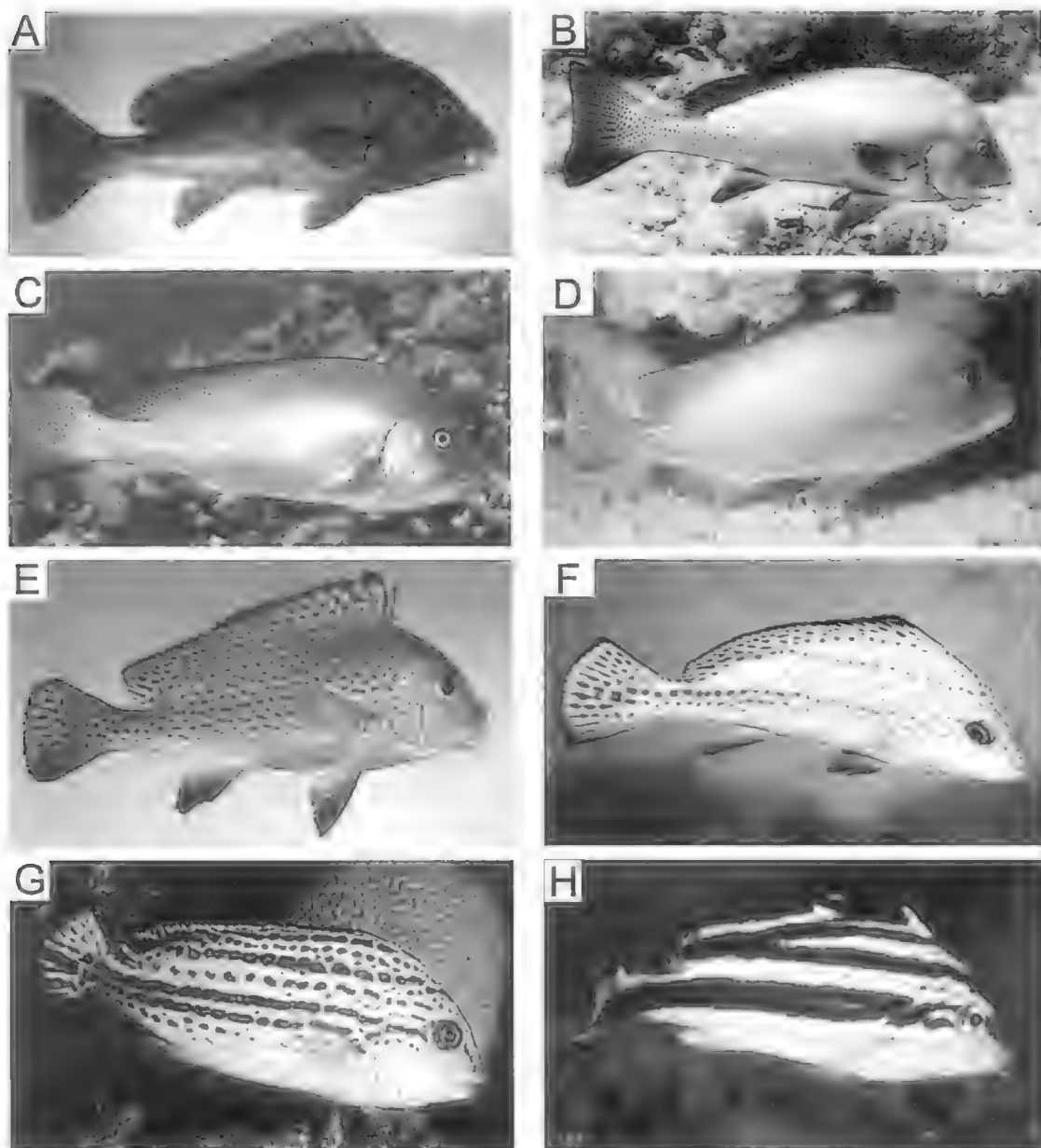


FIG. 6. *Diagramma pictum punctatum*; A, 594mm TL, Sudan, Red Sea, J.E. Randall; B, ~500mm TL, Ras Muhammad, Sinai, Red Sea, H. Debelius; C, ~400mm TL, Daheb, Sinai, Red Sea, J.E. Randall; D, ~300mm TL, Jeddah, Red Sea, G.R. Allen; E, 222mm TL, Nuweiba, Sinai, Red Sea, J.E. Randall; F, ~200mm TL, Egypt, Red Sea, R. H. Kuiter; G, 180mm TL, Red Sea, J.E. Randall; H, 132mm TL, Eilat, Gulf of Aqaba, Red Sea, J.E. Randall.

***Diagramma pictum centurio* Cuvier**
(Common name: East African Slaty)
(Figs 7A-F, 8)

Diagramma centurio Cuvier, 1830 (Seychelles).

REMARKS. *D. pictum centurio* is known from the Seychelles to E Africa and S to Durban. It has been photographed by JWJ (QM NR53, subadult), G.R. Allen (QM NR56, large juvenile), N. Coleman (subadult) and H. Debelius

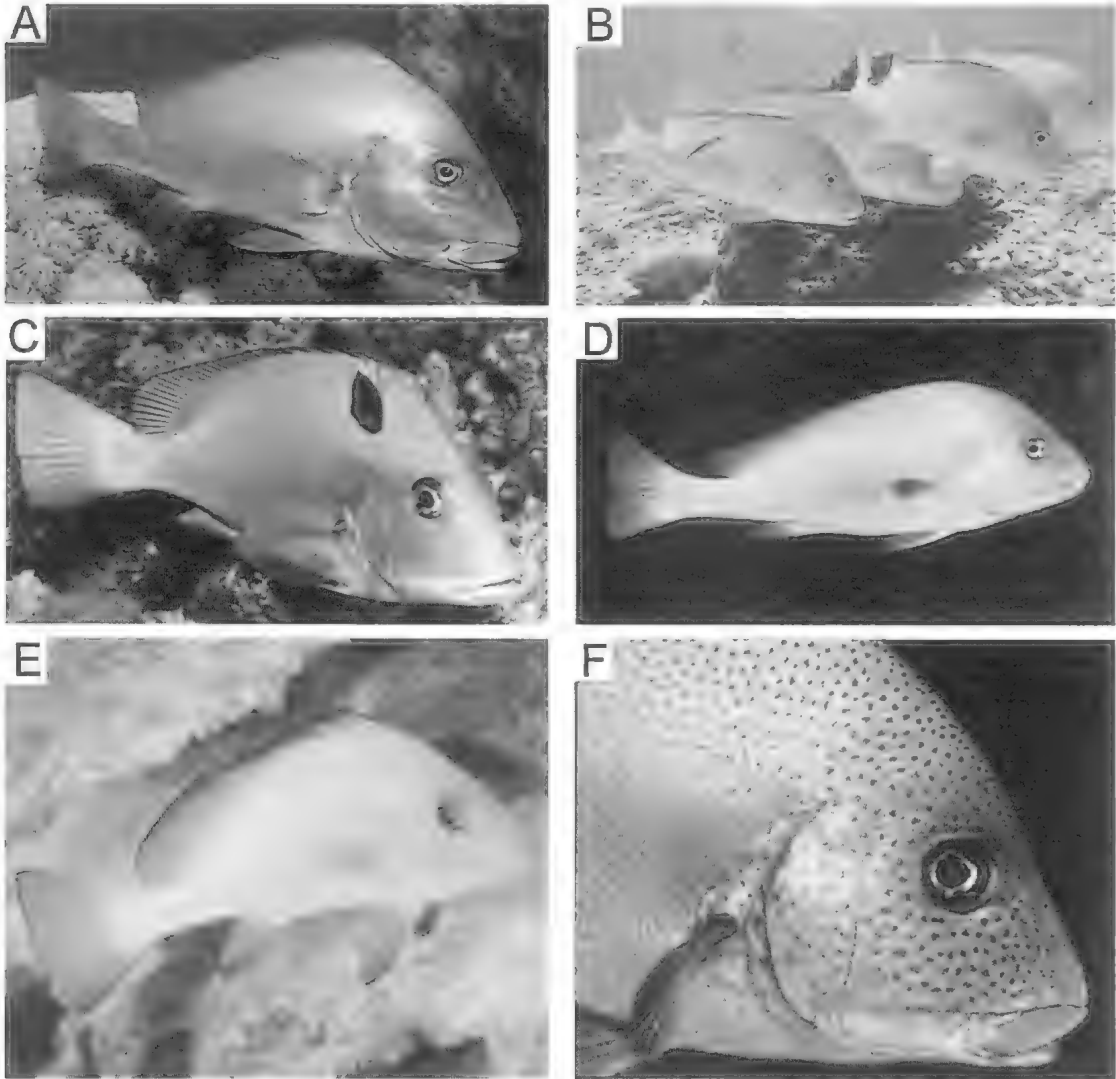


FIG. 7. *Diagramma pictum centurio*; A, ~500mm TL, Mahe, Seychelles, H. Debelius; B, ~350mm TL, Pemba, Kenya, D. Eichler; C, ~250mm TL, Pemba, Kenya, D. Eichler; D, ~300mm TL, Mahe, Seychelles, N. Coleman; E, ~230mm TL, Mahe, Seychelles, G.R.Allen; F, ~200mm TL, Mahe, Seychelles, H. Debelius.

(Debelius, 1999: 99 (adult and juvenile) from Mahe, Seychelles; by D. Eichler (Eichler & Lieske, 1994: 132, from Pemba, Kenya; and a 340mm specimen from Inhaca, Mozambique and a 750mm specimen from Shimoni, Kenya are illustrated (Smith, 1949, pl. 42, fig. 688; Smith, 1962, figs 1, 2).

Cuvier's description of 257mm SL holotype (MNNH8526) of *D. centurio* mentioned scattered small brown spots on the nape, upper body and caudal region. Playfair & Günther (1867) reported a specimen 16 inches from the

Seychelles, with 'head, back, sides, upper part of tail, dorsal and sometimes caudal with brownish-yellow spots'.

No small juveniles from the Seychelles were available for examination, however Debelius (1999: 99 left) illustrated a specimen estimated to be about 200mm TL, with numerous small dark brown spots peppered on the head and upper body. Subadults from this area have slightly larger, sparsely distributed, orange-brown spots on the upper head, body mostly above the lateral line, and on the caudal peduncle. The spots are

smaller than in similar sized *D. pictum pictum*, *D. pictum cinerascens* or *D. pictum punctatum*, and are more sparse than in *D. pictum labiosum*. Adults are slate to silver-grey on the head and body, and may retain a few scattered small spots on the upper body, near the base of the dorsal fin. The soft dorsal and caudal fins may have numerous small close-set dark brown spots, similar to *D. pictum labiosum*.

There appears to be some variability in colouration between individuals from the Seychelles and those from E Africa. Preserved specimens of in excess of 170mm TL from coastal E Africa lack spots on the head and body, and spots on the dorsal and caudal fins, if present, are faint. Fish of this size illustrated in underwater photographs were uniformly silver-grey with no distinctive markings, however few photographs from this region were available for examination. Juveniles are striped to about 150mm TL, but the stripes rapidly regress, forming profuse rows of small dark spots by about 150-160mm TL. Smith's (1949, 1962) figures of a 340mm subadult from Mozambique, however, clearly illustrate fine dark spots on the body and unpaired fins, similar to those in the photograph of Debelius (1999) from Mahe. These spots appear to have been somewhat artist-enhanced in Smith's latter reproduction, but prior to his expedition to the Seychelles in 1954, Smith (1949) alluded briefly to the spots in adults.

Identification of this subspecies is complicated by some variability between regions, however large juveniles (beyond the striped phase) may be peppered with tiny dark brown spots, and the subadult stage may best be distinguished by the presence of small, sparse orange-brown spots on the body. Alternatively, large juveniles and subadults lacking any distinctive markings (some E. African specimens) are separable in that all other subspecies, except some *D. pictum labiosum*, have spots of some type at 160-350mm TL. Also, the median upper, lower and total gill raker counts are highest for all *Diagramma*; the median dorsal ray count (23) is higher than in *D. pictum cinerascens* (22) but lower than in *D. pictum labiosum* (24); and the median lateral-line scale count (59) is lower than in *D. pictum pictum* (65) and *D. pictum labiosum* (69).

DISCUSSION

D. melanacrum is the most distinctive member of the genus, with its low scale count, more robust body and unique colouration. The subspecies of *D. pictum*, although differing considerably in

colouration between one another at certain ontogenetic stages, are remarkably similar as adults. Only *D. pictum pictum* retains obvious spots on the body as an adult. *D. melanacrum* differs from all *D. pictum* subspecies in having the third or fourth dorsal spine longest (second dorsal spine usually longest in the latter, fourth always shorter than second); a taller first dorsal spine, 1.7-2.3 in length of second (2.3-3.9 in the latter); a stouter caudal peduncle, depth of peduncle in its length 2-2.2 (2.2-3.1 in specimens greater than 130mm SL of the latter) and in having pelvic fins that at least reach the vent in all life stages (pelvic fins reach to or slightly beyond the vent in most juveniles up to 200mm SL, but become increasingly remote with growth, large adults falling short by over half length of fin in *D. pictum* subspecies). The tubed lateral-line scale count of 55-57 is lower than that of *D. pictum labiosum* (59-78, usually higher than 65), but overlaps the extreme lower end of the range for other *D. pictum* subspecies (cumulative ranges 55-74). Scale rows above the lateral line to the origin of the dorsal fin, at 14-15, are lower than *D. pictum labiosum* (17-19) and usually lower than other *D. pictum* subspecies (15-18). The range of scale counts for *D. melanacrum*, however, could reasonably be expected to expand when further specimens are available for examination. There are also noteworthy differences in colour. Adults of *D. pictum pictum* have orange to yellow spots on the head and usually also on the body; adults of *D. pictum punctatum* have brown spots on the upper head and body, but they are smaller, more evenly rounded and more sparsely distributed; adults of other *D. pictum* subspecies are slate or silvery-grey, sometimes with large irregular scattered dark blotches. They all lack numerous small close-set dark brown spots on a yellowish background (bronze spots to centres of scales in *D. pictum punctatum* are vague, smaller, lighter in colour and generally follow along the scale rows), and the prominently black lower part of the caudal fin. Other subspecies also usually lack the intensity of black pigmentation to outer part of the anal and pelvic fins, although some juveniles may have dusky fins. *D. melanacrum* is light yellow dorsally on the body, as well as the dorsal fin and upper 3/4 of the caudal fin, and the dark spots on the upper part of the body and on these fins are larger, darker and not arranged one per scale; also there are no large dark blotches on the body.

Diagramma melanacrum appears to be rare compared to most other Indo-Pacific haemulids.

JER has observed it only 3 times in Indonesia and not in the Philippines, Borneo or New Guinea, in spite of many hours underwater at numerous localities in the East Indies region. Nor was it encountered in fish markets. Pieter Bleeker apparently failed to find this species during his many productive years of research on the fishes of Indonesia.

KEY TO *DIAGRAMMA* SPECIES

N.B. Differences in colouration between most subspecies of *D. pictum* is limited mainly to certain ontogenetic stages. Small initial stage juveniles are generally patterned with broad longitudinal black stripes on a cream to creamish yellow background, and are generally not separable using this key. Transformation from striped to spotted colour phases occurs at various lengths between subspecies. Large adults of *labiosum*, *cinerascens* and *centurio* are all generally silver-grey to slate-grey, often with scattered dusky blotches, but differ medially in several meristic features. The colouration of small *D. melanacrum* juveniles is unknown.

1. Lower 1/4-1/3 of caudal fin black; upper body and head with numerous small close-set dark brown spots; third or fourth dorsal spine longest, first dorsal spine 1.7-2.3 in length of second; pelvic fins reaching to or beyond anus; caudal-peduncle depth 2.0-2.2 in its length; tubed lateral-line scales about 55-57 *D. pictum pictum* (Philippines, Borneo, Sulawesi and southern Indonesia)
- Lower 1/4-1/3 of caudal fin not black (often dusky to black near lower margin in juveniles and subadults); upper body and head of adults without small close-set dark brown spots, second dorsal spine usually longest, first dorsal spine 2.3 or more in length of second, pelvic fins not reaching anus in adults (may extend to anus in juveniles); caudal-peduncle depth usually greater than 2.2 in its length; tubed lateral-line scales 55-78 2
2. Lemon yellow, orange to orange-tan spots on head and body of large juveniles and subadults; spots large, 2-6 in eye diameter; adults either lacking spots on the head and body, or with large yellow to orange spots, at least on head; short bars or wavy lines usually on head of large juveniles and subadults; ground colour of median fins often bright yellow in juveniles to subadults; juveniles transform from striped to fully spotted phase at 160-240mm TL 3
- Dark brown, bronze or orange-brown spots on head and body of large juveniles and subadults; spots usually smaller, 4-11 in eye diameter; adults generally silver-grey to slate grey, often with scattered dusky blotches, sometimes with small brown spots, but never with large yellow or orange spots; no short bars or wavy lines on head of juveniles and subadults; ground colour of median fins never bright yellow (except occasionally in initial stage juveniles of up to about 100mm TL); juveniles transform from striped to fully spotted phase at 130-160mm TL 4
3. Tubed lateral-line scales 57-74 (median 65); second and third body stripes of juveniles not merging near pectoral

fin; large yellow to burnt orange spots usually present on head and body of adults (if not, then at least on cheeks); no scattered irregular dusky blotches on head and body of adults; head of subadults and adults usually with combination of spots, short bars and broad wavy lines; spots present on head and body of large juveniles to adults, 2-5 in eye diameter; total gill rakers 19-23 (median 21) *D. pictum pictum* (New Caledonia north to southern Japan and west to the Indo-Malay Archipelago, excluding Australia and southern New Guinea)

Tubed lateral-line scales 55-64 (median 58); second and third body stripes of juveniles merging above posterior half of pectoral fin (in specimens of about 150mm TL); no spots on body of adults; scattered irregular dusky blotches often present on head and body of adults; head of subadults and adults with narrow wavy lines, small spots or unmarked; spots present on head and body of large juveniles to subadults, 3-6 in eye diameter; total gill rakers 17-24 (median 20) *D. pictum cinerascens* (Northern Indian Ocean, from Bay of Bengal to the Persian Gulf)

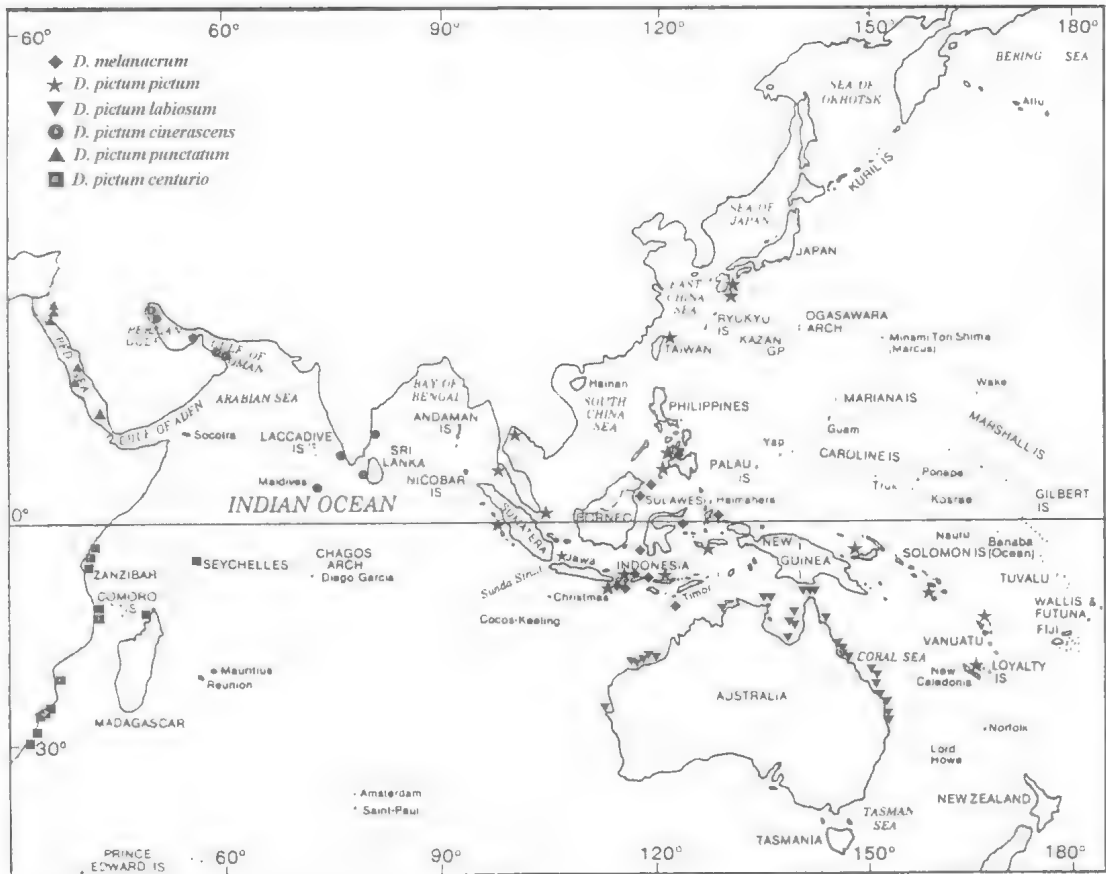
4. Spots on head and body of large juveniles to subadults (180-350mm TL) larger, 4.1-6.6 in eye diameter, often slightly elongate and oblique; adults usually with small scattered round spots on upper head and along body near dorsal fin base and caudal peduncle; adults with small bronze centres to individual scales, forming rows *D. pictum punctatum* (Red Sea)
- Spots on head and body of large juveniles to subadults (180-350mm TL) smaller, 6.5-11.6 in eye diameter, always round, adults either lacking or with only few spots on head and body; adults without small bronze centres to individual scales 5
5. Tubed lateral-line scales 59-78 (median 69); total gill rakers usually 19-21 (median 20); spots on body (when present) bronze to dark brown, always close-set, gradually disappearing from anterior toward posterior part of body with growth, ultimately leaving a small patch of spots at upper part of caudal peduncle, before fading completely *D. pictum labiosum* (northern Australia, from Houtman Abrolhos, WA to Sydney Harbour, NSW; southern New Guinea)
- Tubed lateral-line scales 56-66 (median 59); total gill rakers 21-23 (median 22); spots on body (when present) usually orange-brown, peppered finely in some large juveniles, but sparsely distributed in subadults; not gradually disappearing from anterior toward posterior part of body with growth, not leaving a small patch of spots at upper part of caudal peduncle, before fading completely *D. pictum centurio* (East Africa to Seychelles)

OTHER MATERIAL EXAMINED

(Fig. 8)

(Numbers in brackets are lengths of specimens in mm. Catalogue numbers refer to single specimens unless otherwise indicated by number in italics)

D. pictum labiosum. QUEENSLAND: QMI3371 (148); QMI3442 (124); QMI3946 (203); QMI6079 (187); QMI6678 (163); QMI7094 (261); QMI7579 (238); QMI7804 (283); QMI7853 (115); QMI11555 (266); QMI12535 (129); QMI12536 (127); QMI12710 (268); QMI12616 (292); QMI12724-30.7 (224-337); QMI12908

FIG. 8. Confirmed distributional records of examined *Diagramma* species

2 (117-119); QMI15058 (156); QMI15097 (118); QMI15965 (98); QMI16467 (116); QMI16852 2 (96-127); QMI20132 (192); QMI20850 (107); QMI20884 (123); QMI21223 (110); QMI21334 (151); QMI23229 2 (84-126); QMI30757 (401); QMI30758 (434); QMI30759 (370); QMI30760 (380); QMI30761 (601); QMI30762 (620); BPBM14335 (349); BPBM14465 (138). Northern Territory: NTMS10577-001 (222); NTMS11613-028 (356); NTMS13318-002 3 (175-213). WESTERN AUSTRALIA: QMI10225 2 (83-105); QMI14230 (112); QMI30726 2 (123-196); QMI30727 (255); QMI30728 (232); QMI30729 (238); QMI31110 (468); QMI31111 (519); QMI31112 (511); NTMS10987-002 (436); CSIROH3834-02 (341).

D. pictum pictum. JAPAN: MUFS12534 (192); MUFS12847 (245); MUFS11816-7 2 (136-156.5); MUFS12162 (142); MUFS12226 (114.5); QMI31403-4 2 (372-377). INDONESIA: BMNH1858.4.21:364 (85); QMI20383 (304); QMI20284 (136); QMI20286 (100); QMI20287 (186); QMI20288 (503); QMI20289 (302); QMI20304 (61); BPBM36675 (38); BPBM18593 (99); BPBM20678 (239); BPBM30100 2 (60-61); NTMS11037-001 (332); NTMS11127-016 (95).

THAILAND: QMI21687 12 (58-212); PMBC14425 (152); PMBC5884 (190), PMBC5885 (185), PMBC5890 (175) and PMBC5891 (187). MALAYSIA: AMIA3343 (94); QMI30873 (311); QMI30874 (325); QMI31076 3, 136-188); QMI31113 (224). PHILIPPINES: AMI10568 (118); AMI10503 (120); BPBM28550 (95); BPBM22143 (187). TAIWAN: BPBM18687 (200). VANUATU: AMI17142-015 (173). NEW CALEDONIA: AMIB2410 (275). SOLOMON ISLANDS: BPBM17371 2 (172-245). PAPUA NEW GUINEA: BPBM15709 (104).

D. pictum cinerascens. INDIA: AMI15599-006 (125); AMB8320 (141); BMNH1888.11.6:7-8 2 (147-181); BMNH1889.2.1:2961 (45); BMNH1847.11.22:134-136 2 (74-90); BPBM20666 2 (67-86); PMBC5886 (181), PMBC5887 (181), PMBC5892 (167), PMBC5893 (169) and PMBC5894 (197). GULF OF OMAN: BMNH1888.12.29:48 (172). PERSIAN GULF: BMNH1904.5.25:184 (78); BMNH2000.4.19:1113 (155); BPBM33174 (68); BPBM21181 3 (63-132); BPBM29495 3, 117-144).

D. pictum punctatum. RED SEA: BMNH 1860.11.9:93 (157); BMNH1960.3.15:763 (36); BMNH1871.4.13:9 2,

(192-237); RUSI7989 2 (113-128); BPBM19856 (180); BPBM31867 (100).

D. pictum venturio. SEYCHELLES: AMJ32067-001 (232). KENYA: RUSI41682 (168); RUSI41677 2, (50-61). TANZANIA: BMNH1985.7.9:193 (203). MOZAMBIQUE: RUSI41656 4, (59-125); RUSI41681 (161); RUSI41680 (141); RUSI4227 (127); RUSI41679 (122); RUSI56386 2, (98); RUSI41678 (76). MADAGASCAR: RUSI52829 10, 73-105). SOUTH AFRICA: RUSI3846 (68); RUSI12754 (46); BMNH1919.9.12:24 (193).

ACKNOWLEDGEMENTS

We are grateful to Klaus E. Fiedler, Dieter Eichler, Rudie H. Kuiter and J. Barry Hutchins for providing underwater photographs of *D. melanacrum*. Rudie H. Kuiter, R. Charles Anderson, Dieter Eichler, Helmut Debelius, Gerald R. Allen, Philip Woodhead, Neville Coleman and John Hoover provided photographs of various phases of *D. pictum*. Phillip C. Heemstra and Andrew Bentley of the JLB Smith Institute of Ichthyology, Chhatsee Angtanya of the Phuket Marine Biological Centre, Anthony C. Gill of the Natural History Museum, Yukio Iwatsuki and Hiroyuki Motomura of the Miyazaki University, Helen K. Larson of the Northern Territory Museum and Mark A. McGrouther of the Australian Museum made available comparative material of *Diagramma* under their care. Alastair Graham of the Division of Fisheries of CSIRO, Hobart arranged for fresh specimens to be sent from WA and sent a duplicate colour slide of the holotype of *D. melanacrum* taken by Thomas Gloerfelt-Tarp. Patricia J. Kailola kindly gave us permission to reproduce this photograph herein. Peter K.L. Ng and Thomas Tan Han Tong sent fresh specimens from Singapore and Michael McDade collected specimens from North West Island. Special thanks are due to Roland J. McKay of the Queensland Museum for assistance in the description of *D. melanacrum*.

LITERATURE CITED

- ALLEN, G.R. 1993. Part 7. Fishes of Ashmore Reef and Cartier Island. Records of the Western Australian Museum Supplement 44: 67-91.
- ALLEN, G.R. & STEENE, R.C. 1987. Pacific marine fishes, Book 10. Reef fishes of the Indian Ocean. (T.F.H. Publications: Neptune City, New Jersey).
- WISE, J.C. 1994. Molecular markers, natural history and evolution. (Chapman and Hall: New York).
- WISE, J.C., BERMINGHAM, E., KESSLER, L.G. & SAUNDERS, N.C. 1984. Characterization of mitochondrial DNA variability in a hybrid swarm between subspecies of bluegill sunfish (*Lepomis microchilus*). Evolution 38(5): 931-941.
- BAUCHOT, M.L., DESSOUTTER, M. & MCKAY, R.J. 1983. Catalogue critique des types de poissons du Museum national d'Histoire naturelle (Suite) (Familles des Haemulidae et des Sillaginidae). Bulletin Museum National d'Histoire Naturelle, ser. 4, section A, 5(2) supplement: 27-61.
- BURGESS, W.E. & AXELROD, H.R. 1972. Pacific marine fishes, Book 1. (T.F.H. Publications: Neptune City, New Jersey).
1974. Pacific marine fishes, Book 5, pp. 1111-1381. Fishes of Taiwan and adjacent waters. (T.F.H. Publications: Neptune City, New Jersey).
1975. Pacific marine fishes, Book 6, pp. 1383-1654. Fishes of Melanesia. (T.F.H. Publications: Neptune City, New Jersey).
1976. Pacific marine fishes, Book 7, pp. 1655-1925. Fishes of the Great Barrier Reef. (T.F.H. Publications: Neptune City, New Jersey).
- BURGESS, W.E., H.R. AXELROD & R.F. HUNZIKER III 1988. Dr Burgess's atlas of marine aquarium fishes. (T.F.H. Publications: Neptune City, New Jersey).
- COLEMAN, N. 1980. Australian sea fishes south of 30 S. (Doubleday Australia: Sydney).
- CUVIER, G. & VALENCIENNES, A. 1830. Histoire naturelle des poissons Vol. 5 (10), Paris-Strasbourg.
- DAY, J. 1878-88. The fishes of India; being a natural history of the fishes known to inhabit the seas and fresh waters of India, Burma, and Ceylon. (Cl Norman & Son: London).
- DEBELIUS, H. 1993. Indian Ocean tropical fish guide (Aquaprint: Neu Isenburg, Germany).
1998. Red Sea reef guide. (Ikan-Unterwasserarchiv, Frankfurt).
1999. Indian Ocean reef guide. (Ikan-Unterwasserarchiv: Frankfurt).
- EICHLER, D. & LIESKE, E. 1994. Korallenfische Indischer Ozean. (Jahr-Verlag: Hamburg).
- EICHLER, D. & MYERS, R.F. 1997. Korallenfische Zentraler Indopazifik. (Jahr-Verlag: Hamburg).
- ESCHMEYER, W.N. 1998. Catalogue of fishes, Vol. 1-3. (California Academy of Sciences: San Francisco).
- FOURMANOIR, P. & LABOUTTE, P. 1976. Poissons de Nouvelle Calédonie et des Nouvelles Hébrides. (Les Editions du Pacifique: Papeete, Tahiti).
- FOWLER, H.W. 1931. Contributions to the biology of the Philippine Archipelago and adjacent regions. The fishes of the families Pseudochromidae, .. adjacent waters. Bulletin of the United States Museum 100, Vol. 11: 1-388.
- GLOERFELT-TARP, T. & KAILOLA, P.J. 1984. Trawled fishes of southern Indonesia and northwestern Australia. The Australian Development Assistance Bureau; The Directorate General of Fisheries, Indonesia; and The German Agency for Technical Cooperation.

- GRANT, E.M. 1982. Guide to fishes. (Department of Harbours and Marine: Brisbane).
1987. Fishes of Australia. (E.M. Grant: Scarborough, Australia).
- KUITER, R.H. 1993. Coastal fishes of south-eastern Australia. (Crawford House Press: Bathurst, Australia).
1996. Guide to sea fishes of Australia. (New Holland Publishers: Sydney).
1998. Photo guide to fishes of the Maldives. (Atoll Editions: Apollo Bay, Victoria).
- KUITER, R.H. & DEBELIUS, H. 1994. Southeast Asia tropical fish guide. (Ikan Unterwasserarchiv: Frankfurt).
- McELROY, D., MORAN, P., BERMINGHAM, E. & KORNFIELD, I. 1996. Appendix: Programs and software packages available for conducting phylogenetic and population genetic analyses. P. 514. In Hillis, D.M., Moritz, C. & Mable, B.K. 1996, *Molecular Systematics*. (Sinauer Associates: Massachusetts).
- McKAY, R.J. 1983. Haemulidae. In Fischer, W. & Bianchi, B. (eds) *FAO species identification sheets for fishery purposes. Western Indian Ocean (Fishing Area 51). Vol. 2.* (Food and Agriculture Organisation of the United Nations: Rome).
- MACLEAY, W. 1883. Notes on a collection of fishes from the Burdekin and Mary rivers, Queensland. *Proceedings of the Linnean Society of New South Wales* 8(2): 199-213.
- McMILLAN, W.O. & PALUMBI, S.R. 1995. Concordant evolutionary patterns among Indo-Pacific Butterflyfishes. *Proceedings of the Royal Society of London*, B. 260: 229-236.
- MASUDA, H. 2000. Field guide to sea fishes. (Tokai University Press: Tokyo).
- MASUDA, H., AMAOKA, K., ARAGA, C., UYENO, T. & YOSHINO, T. 1984. Pl. 1-370. In *The fishes of the Japanese Archipelago*. (Tokai University Press: Tokyo).
- MASUDA, H. & KOBAYASHI, Y. 1994. Grand atlas of fish life modes: color variation in Japanese fish. (Tokai University Press, Tokyo).
- MYERS, R.F. 1999. Micronesia reef fishes. (Coral Graphics: Guam).
- NEI, M. 1987. *Molecular evolutionary genetics*. (Columbia University Press: New York).
- OKAMURA, O., AMAOKA, K. & OKATA, Y. 1997. *Sea fishes of Japan*. (Yama-kei Publishers: Tokyo).
- PALUMBI, S.R., MARTIN, A., ROMANO, S., McMILLAN, W.O., STICE, L. & GRABOWSKI, G. 1991. *The simple fool's guide to PCR*. (Department of Zoology, University of Hawaii: Honolulu).
- PLAYFAIR, R.L. & GÜNTHER, A.C.L.G. 1867. *The fishes of Zanzibar*. (John Van Voorst: London).
- RANDALL, J.E. 1983. *Red Sea reef fishes*. (Immel Publishing: London).
1992. *Divers guide to fishes of Maldives*. (Immel Publishing: London).
1995. *Coastal fishes of Oman*. (Crawford House Press: Bathurst, Australia).
- RANDALL, J.E., ALLEN, G.R. & STEENE, R.C. 1990. *Fishes of the Great Barrier Reef and Coral Sea*. (Crawford House Press: Bathurst).
1997. *Fishes of the Great Barrier Reef and Coral Sea*. (Crawford House Press: Bathurst).
- RÜPPELL, W.P.E.S. 1830. *Atlas zu der reise im nordlichen Afrika, fische*. (Fische des Rothen Meeres: Frankfurt).
- SAINSBURY, K.J., KAILOLA, P.J. & LEYLAND, G.G. 1985. *Continental shelf fishes of northern and north-western Australia*. (Clouston & Hall & Peter Pownall Fisheries Information Service: Canberra).
- SAMBROOK, J., FRITSCH, E.F. & MANIATIS, T. 1989. *Molecular cloning: a laboratory manual*. (Cold Spring Harbour Laboratory Press: New York).
- SHEN, S.C. 1984. *Coastal fishes of Taiwan*. (Shih-Chieh Shen, National Taiwan University: Taipei).
- SMITH, J.L.B. 1949. *Sea fishes of southern Africa*. (Central News Agency: South Africa).
1962. Fishes of the family Gaterinidae of the western Indian Ocean and the Red Sea with a resume of all known Indo Pacific species. *Ichthyological Bulletin of the Rhodes University* 25: 469-502.

NEW OCTOPUS SPECIES FROM QUEENSLAND

MARK D. NORMAN

Norman, M.D. 2001 06 30: New octopus species from Queensland. *Memoirs of the Queensland Museum* 46(2): 677-690. Brisbane. ISSN 0079-8835.

Three new octopus species are added to the growing list of Australian octopods. All are known solely on the basis of trawl material from habitats not easily surveyed using standard diving techniques. *Octopus harpedon* sp. nov. attains arm spans in excess of 2m. It occurs in shallow muddy waters in the Gulf of Carpentaria. *Octopus bulbus* sp. nov. is also a long-armed species, which possesses a swollen bulbous ligula and a skin ridge around the lateral mantle. *Octopus micros* sp. nov. is tiny (mature at <25mm mantle length), the first pygmy species to be reported with a lateral mantle ridge. The latter 2 species occur on the continental shelf off southern Queensland in water depths of 18-195m and 166-195m, respectively. The phylogenetic affinities and potential life styles of these octopuses are discussed in light of their morphological attributes. □ *Octopus*, taxonomy, morphology; Queensland, Cephalopoda.

Department of Zoology, University of Melbourne, Parkville 3052, Australia; Present address: Marine Invertebrates, Melbourne Museum, GPO Box 666E, Melbourne, 3001, Australia (e-mail: m.norman@unimelb.edu.au); 17 March 2000.

Research into benthic octopuses of Australia and the Indo-West Pacific region over the past decade has revealed more than 70 new species of octopus in Australian waters (Stranks, 1988a-b, 1990; Norman, 1992, 1993a-d, 1998; Stranks & Norman, 1993; Norman et al., 1997; Norman, unpubl. data), the bulk of which await formal description. Within this fauna are 3 distinctive and very different octopus species from Queensland waters.

The 'Spaghetti Octopus', *Octopus harpedon* sp. nov. is reported from the shallow waters of the Gulf of Carpentaria. This octopus has extremely elongate arms (up to 10 times mantle length) and would attain arm spans of >2m when foraging over its soft sediment habitat.

The other two species were collected from continental shelf waters (>150m) off the south coast of Queensland. The 'Swell-Club Octopus', *Octopus bulbus* sp. nov., is also long-armed (arms to 5 times mantle length) with a distinctive swollen ligula. Arm spans of live animals would be up to 50cm. This species possesses a distinctive lateral mantle ridge.

The 'Pygmy Keeled Octopus', *Octopus micros* sp. nov., is tiny with an arm span of <12cm and a weight of <6g. It is the first pygmy species to be reported with a lateral mantle ridge.

There are few specimens available for these species, all originating from trawl surveys. None of these new species have been observed live. Based on the available material, the taxonomic

affinities and potential habits of these little-known creatures are discussed.

SYSTEMATICS

FAMILY OCTOPODIDAE

Octopus harpedon sp. nov. (Figs 1-2, 9A-B, 10A-C)

MATERIAL. HOLOTYPE: 1♂, 56.9mm ML, AMC30411, Albatross Bay, near Weipa, Gulf of Carpentaria. PARATYPE: 1♀, 96.1mm ML, AM C304112, SE Gulf of Carpentaria, 16°27'40"S, 141°15'25"E, 2m.

TYPE LOCALITY. Albatross Bay, near Weipa, Gulf of Carpentaria, Australia

ETYMOLOGY. Greek *harpedon*, thread-like; referring to elongate, thread-like arms. "Spaghetti Octopus" is proposed as a common name.

DIAGNOSIS. Moderate-sized (ML to 96mm) with spindle-shaped mantle and bulbous eyes. Arms greatly elongate, up to 9 times mantle length. Second arm pair appears longest (arm formula approximately 2>1=3>4). Webs very shallow, less than 5% of arm length. Approximately 270 suckers on intact arms of mature animals. Third right arm of male hectocotylised, very short (only 20% of length of opposite arm) and bearing 49 suckers. 10-11 gill lamellae per demibranch. Eggs large-type. Skin largely unpigmented, dark blue subdermal pigment around eyes produces 'bruised' appearance. Skin smooth. Lateral ridge absent.



FIG. 1. *Octopus harpedon* sp. nov. (♂ holotype, AMC30411). A, dorsal view (scale bar = 30mm); B, mantle and arm crown (scale bar = 30mm); C, copulatory organ (scale bar = 2mm).

DESCRIPTION. Counts and measurements were taken off a single specimen of each sex, the only known specimens of this distinctive species. Raw morphological data are presented in Table 1.

Moderate sized species with extremely long arms (Figs. 1A-B, 9A-B); mantle lengths (ML) 56.9mm for male holotype and 96.1mm for female paratype. Total length of ♂ 394mm and ♀ 997mm; weight to at least 104g. Mantle elongate to spindle-shaped, much longer than wide (♂: width 35.1% of ML; ♀: width 24.9% of ML), mantle walls thin to moderately muscular. Head narrower than mantle (♂: 26.4% of ML, 75.0% of mantle width; ♀: 15.8% of ML, 63.6% of mantle width). Eyes moderate to small, only slightly pronounced. Stylets absent. Mantle aperture of moderate width, approximately half circumference of body at level of opening. Funnel narrow and elongate, approximately 50% of mantle length (♂: 51.5% of ML; ♀: 47.9% of ML). Free portion short, approximately one third of funnel length (♂: 23.9% of funnel length; ♀:

33.5% of funnel length). Funnel organ not evident in either specimen.

Arms extremely long, longest >5 times mantle length (♂: $5.9 \times \text{ML}$; ♀: $9.1 \times \text{ML}$). Arms narrow relative to mantle length (♂: 9.3% of ML; ♀ [ex frozen]: 5.9% of ML), widest midway along arm, roughly square in cross section. Arms unequal in length, ventral pair distinctly shortest, second pair appears longest (arm formula: ♂: $\sim 2 > 1 > 3 > 4$, ♀: $\sim 2 > 1 = 3 > 4$). Suckers in two rows and of moderate size (♂: 7.0% of ML, ♀: 5.0% of ML), slightly elevated with only slight flare. No enlarged suckers evident in either sex. Approximately 280 suckers on intact arms of mature animals (♂: 272 suckers on left third arm; ♀: 291 suckers on left third arm). Webs tiny, shortest relative to arm length reported for any octopus (♂: deepest web 3.9% of longest arm; ♀: deepest web 2.4% of longest arm). Web sectors approximately equal in length. Web margins along arms absent.

Third right arm of males hectocotyliised. Modified arm very short, less than mantle length (79.1% of ML), and around 20% of length of opposite arm (20.4% of opposite arm). Ligula moderate-size (7.3% of arm length, 5.8% of mantle length), in the form of a small thick-lipped spoon with transverse creases across the open ligula groove (Fig. 1C). Calamus distinct and sharp, approximately one half of ligula length (54.6% of ligula). Spermatophore groove well developed and wide with fine transverse creases. Spermatophore guide distinct with a ridge of elevated square papillae. Forty-nine suckers on hectocotyliised arm of single male.

Gills with 10-11 lamellae on both inner and outer demibranchs, plus terminal lamella.

Digestive tract (Fig. 2A). Anterior salivary glands extend along approximately one third of buccal mass from posterior margin on dorsal surface. Posterior salivary glands elongate and of moderate length (similar in length to buccal mass, approximately 30% of digestive gland length). Crop diverticulum present, long and narrow. Stomach bipartite. Caecum coiled in approximately 1.5 whorls with distinct striations. Digestive gland long and narrow, not bound in an iridescent membrane. Narrow intestine reflexed several times in proximal third. Ink sac well developed, embedded in ventral surface of digestive gland. Anal flaps absent. Upper beak with a hooked rostrum, concave and notched on the cutting edge, and a small hood (Fig. 2B). Lower beak with narrow short rostrum, hood

narrow, widely spread wings and slightly flared lateral walls (Fig. 2C-D). Radula with 7 teeth and 2 marginal plates in each transverse row (Fig. 10A-C). Rhachidian tooth with 2-3 lateral cusps, on each side of moderately long medial cone (Fig. 10A). Lateral cusps in asymmetrical seriation, migrating from lateral to medial position over 7-8 transverse rows (Fig. 10B). First lateral teeth unicuspidate with cusp towards lateral edge. Second lateral teeth unicuspidate and long with curved base. Lateral marginal teeth straight. Marginal plates oblong and plain (Fig. 10C).

Male genital tract not fully formed. Submature terminal organ ('penis') T-shaped with diverticulum slightly longer than distal portion.

Female genital tract not fully formed but eggs in tiny ovary already large and low in numbers (<100). This species would produce large eggs and the young are likely to be benthic on hatching. Oviducts elongate, opening posterior to the narrow short septum.

Colour in life unknown. Preserved specimens uniformly cream (♀) and pink (♂) with dark subdermal pigmentation around the eyes of both specimens giving a 'bruised' appearance (Fig. 1B). Dorsal White Spots (*sensu* Packard & Sanders, 1971) absent. Skin smooth. Lateral mantle ridge absent. Nothing is known of the behaviour and general biology. The short hectocotylised arm of the ♂ suggests mounted copulation in this species as opposed to other octopus species where a long hectocotylised arm enables copulation from a distance (as found in other long-armed species such as *O. aculeatus*, Norman & Finn, 2001). Numerous spiral parasites were present along sections of the digestive tract, particularly adjacent to the crop and intestine.

TAXONOMIC REMARKS. Only one other Australian octopus has arms of comparable relative length. *Ameloctopus litoralis* Norman, 1992 is an intertidal, smaller species (ML to 30mm) with arms up to 10 times the mantle length. It is distinguished from *O. harpedon* in that it has a much lower gill count (5-6 versus 10-11 lamellae per demibranch), a linear terminal organ which lacks a diverticulum, distinctive bands along the arms (compared with little pigmentation in *O. harpedon*), and it lacks an ink sac.

An undescribed octopus from Hong Kong, China and Taiwan also shows similarities to this new species, sharing similar arm lengths and gill

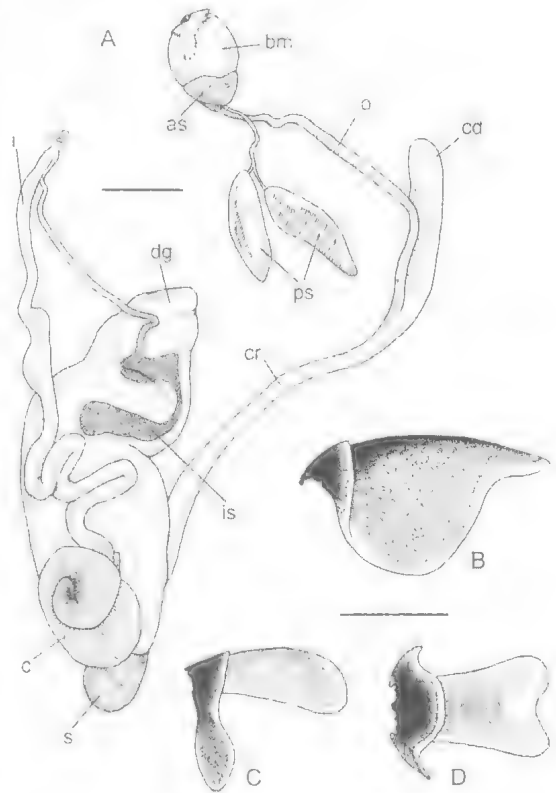


FIG. 2. *Octopus harpedon* sp. nov. A, digestive tract (♀, AM C304112): as = anterior salivary glands, bm = buccal mass, c = caecum, cd = crop diverticulum, cr = crop, dg = digestive gland, i = intestine, is = ink sac, o = oesophagus, ps = posterior salivary gland, s = stomach (scale bar = 10mm). B-D, beaks (♂ holotype, AM C30411) (scale bar = 3mm); B, upper beak, lateral view; C, lower beak, lateral view; D, lower beak, ventral view.

counts. This Asian taxon has been treated under a number of names by various authors: *Octopus* sp. B. Voss & Williamson, 1972; *Octopus fusiformis* (non Brock, 1887) in Dong, 1987; *Octopus* sp. 1 Norman & Hochberg, 1994. It can be distinguished from *O. harpedon* on the basis of differences in arm formula (1>2>3>4 versus second pair longest in *O. harpedon*) and hectocotylised arm length (~50% versus 20% of opposite arm length in *O. harpedon*). Additional mature material of both taxa is required to further resolve the relationship between these octopuses.

As for higher taxonomic affinities, *O. harpedon* shares a number of characters with poorly-known *Euaxoctopus* Voss, 1971. *Euaxoctopus* contains 2 quite different species from

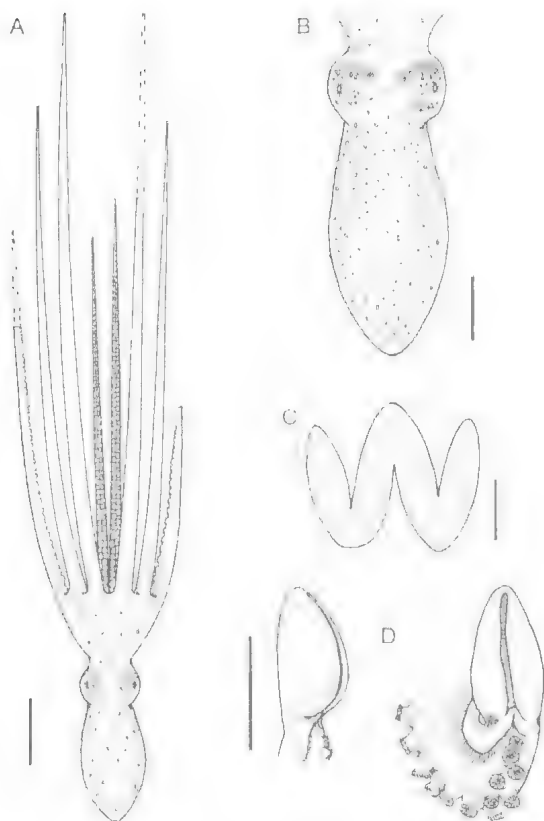


FIG. 3. *Octopus bulbus* sp. nov. (♂ holotype, MV F87067); A, dorsal view (scale bar = 20mm); B, mantle (scale bar = 10mm); C, funnel organ (scale bar = 5mm); D, copulatory organ (scale bar = 5mm).

either side of the Panama Isthmus. *E. pillsburyae* Voss, 1971 and *E. panamensis* Voss, 1975 share long arms of which the second pair are longest, shallow webs, paired semi-circular ocelli on the mantle, a large crop, a rhachidian tooth of the radula with 1-2 lateral cusps on each side (typically 1), a blunt linear terminal organ with a diverticulum longer than the distal free portion, and distinctive spermatophores with flattened coils in the oral tip. The two member species differ in that *E. panamensis* has a hectocotylised left arm, a gill count of 11-13 lamellae, and a VV-shaped funnel organ, while *E. pillsburyae* has the right third arm hectocotylised, a gill count of 7, and a W-shaped funnel organ. *Octopus harpedon* shares the same arm formula (second pair longest) and blunt linear terminal organ with a diverticulum longer than the distal free portion. It differs in lacking the semicircular ocelli on the mantle and possesses a radula with a higher number of lateral cusps on the rhachidian tooth

(2-3 per side). In the absence of mature material of *O. harpedon* spermatophores can not be compared. The disparate composition of *Euxoctopus* and the absence of replicate well-preserved material for both this genus and *O. harpedon* prevent further resolution of their affinities. Based on available material, I place this species in *Octopus*.

Octopus harpedon shares several morphological characters with the '*Octopus macropus* group' (Norman, 1993a). This group is characterised by an arm formula of $1>2>3>4$, high gill counts (10+ lamellae per demibranch) and a rhachidian tooth of the radula with 2-3 cusps on each side of the medial tooth, migrating from medial to lateral positions over 7-8 transverse rows. The radula and gill count of *O. harpedon* match those of the *Octopus macropus* group but arm length, arm formula and ligula shape differ.

Until more material becomes available (including fresh tissue for molecular analyses), the higher affinities of this distinctive octopus remain unknown.

***Octopus bulbus* sp. nov.**
(Figs 3-5, 9C, 10D-F)

MATERIAL. HOLOTYPE: 1♂: 41.1mm ML, MV F87067, east of Mooloolaba, 16-20 miles north of Cape Moreton, southern Queensland, 90-106fm (166-195m), trawl, FV 'Debie-Marie', 11-13 Aug 1981, coll. G. Smith, Queensland Fisheries. PARATYPES: 1♂: 53.0mm ML, MV F87068, East of Noosa, southern Queensland, 63fm (116 m), trawl, FV 'Rhonda Lane', 12 Dec 1980, coll. M. Potter, Queensland Fisheries; 1♀: 49.2mm ML, MV F87069, off Mooloolaba, southern Queensland, 10fm (18.4m), trawl, 1500-1600hrs, FV 'Rhonda Lane', 14 Dec 1980, coll. M. Potter, Queensland Fisheries.

TYPE LOCALITY. East of Mooloolaba, southern Queensland, Australia.

ETYMOLOGY. Latin *bulbus*, fleshy swelling; referring to the distinctive swollen ligula. 'Bulb-tip Octopus' is proposed as a common name.

DIAGNOSIS. Small (ML to 50mm) with relatively long arms, approximately 5 times mantle length. Dorsal arms longest, receding to ventral arm pair (arm formula $1>2>3>4$). 7-8 gill lamellae per demibranch. Approximately 200 suckers on intact arms. Third right arm of ♂♂ hectocotylised, bearing approximately 90 suckers. Posterior salivary glands large and elongate (almost twice length of buccal mass, approximately 60% of digestive gland length). Ligula large (8% of hectocotylised arm length)

with greatly swollen lips to the ligula groove. Spermatophores thick and short, approximately half mantle length. Dorsal mantle and arm crown sculptured with scattered pink-red raised patches. Lateral ridge present.

DESCRIPTION. Counts and measurements were taken off the only known specimens, 2 mature ♂♂ and a submature ♀. Morphological data are presented in Table 1.

Moderate-sized elongate (Fig. 3A); mantle length to around 50mm (♂: to 53.0mm ML, ♀: 49.2mm ML). Total length to 341mm; weight to at least 47g. Mantle elongate to spindle-shaped, much longer than wide (width 53.5% of ML in holotype, other material distorted from freezing), mantle walls moderately muscular. Head approximately same width as mantle (53.3% of ML, 99.5% of mantle width in holotype, other material distorted from freezing). Eyes large and pronounced. Stylets absent. Mantle aperture of moderate width, approximately half circumference of body at level of opening. Funnel broad-based, approximately one half of mantle length (41.8–62.2% of ML), free portion elongate, 32.1–56.0% of funnel length. Funnel organ W-shaped with broad limbs (Fig. 3A). Outer limbs slightly shorter in length than median limbs (outer limbs 86.4% of median limbs in holotype). Funnel organ occupies approximately two thirds of funnel length (59.8% of funnel length).

Arms long, approximately 5 times mantle length (longest 4.9–5.6 × ML). Arms of moderate width relative to mantle length (13.9% of ML), widest at one third of arm length from base then tapering evenly to tip, roughly square in cross section. Arms unequal in length, dorsal pair longest (arm formula: 1>2>3>4). Suckers in 2 rows and of moderate size (6.7–9.8% of ML), slightly elevated with low flare and a deep cup. No enlarged suckers evident in either sex. Approximately 190 suckers on intact arms of mature animals (196 suckers on fourth right arm of holotype). Webs shallow and thin (deepest web 10.9–11.5% of longest arm in intact specimens). Dorsal and lateral web sectors approximately equal in length, ventral webs shallower (web formula A=B=C>D>E). Web margins extend along both dorsal and ventral aboral edges of arms for less than one third of the arm length.

Third right arm of ♂♂ hectocotylised. Modified arm relatively short, almost half as long as normal arms (2.0–2.5 × ML, 56.3% of opposite arm). Ligula large (8.0–8.6% of

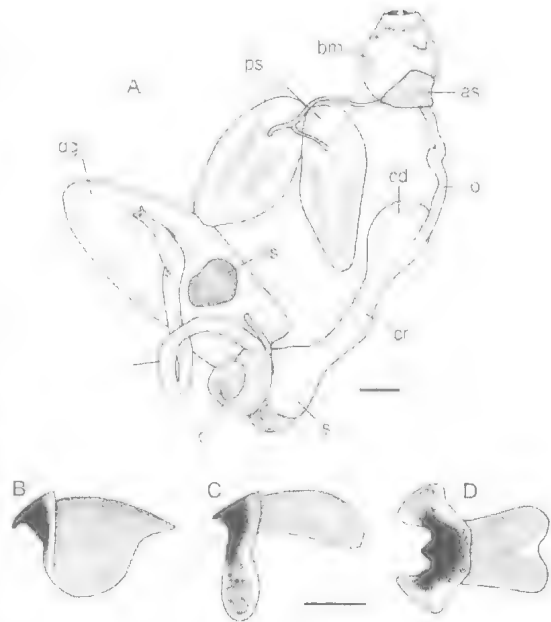


FIG. 4. *Octopus bulbus* sp. nov. digestive system (♀ paratype, MV F87068); A, digestive tract: symbols as in Fig. 2 (scale bar = 5mm). B–D, beaks; B, upper beak, lateral view; C, lower beak, lateral view; D, lower beak, ventral view (scale bar = 3mm).

hectocotylised arm length, 16.1–21.9% of mantle length), in the form of an elongate oval with a deep closed groove (Fig. 3C–D). Calamus small and sharp, <20% of ligula length (17.2–18.2% of ligula). Spermatophore groove well developed, of moderate width with fine transverse creases. Spermatophore guide not obvious. Approximately 90 suckers on hectocotylised arm (91, 94).

Gills with 7–8 lamellae on both inner and outer demibranchs, plus terminal lamella.

Digestive tract (Fig. 4A). Anterior salivary glands extend along approximately one third of buccal mass from posterior margin on dorsal surface. Posterior salivary glands large and elongate (almost twice length of buccal mass, approximately 60% of digestive gland length). Crop diverticulum present, moderately small. Stomach bipartite. Caecum coiled in 1.5 whorls, with distinct striations. Digestive gland approximately ovoid. Muscular intestine reflexed approximately one third along length from proximal end. Ink sac well-developed, embedded in ventral surface of digestive gland. Anal flaps present, small. Upper beak with a hooked rostrum, concave on cutting edge, and moderate

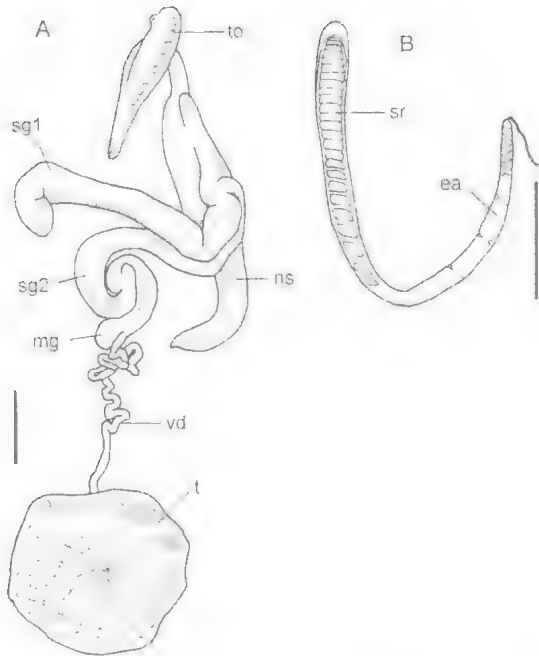


FIG. 5. *Octopus bulbus* sp. nov. reproductive system (δ holotype, MV F87067). A, reproductive tract: mg = mucilagenous gland, ns = Needham's sac, sg1 = spermatophoric gland, sg2 = accessory spermatophoric gland, t = testis, to = terminal organ ('penis'), vd = vas deferens (scale bar = 5mm); B, spermatophore: ea = ejaculatory apparatus; sr = sperm reservoir (scale bar = 5mm).

hood (Fig. 4B). Lower beak with pointed rostrum, narrow hood, widely-spread wings and slightly flared lateral walls (Fig. 4C-D). Radula with 7 teeth and 2 marginal plates in each transverse row (Fig. 10D-F). Rhachidian tooth with 2-3 lateral cusps, typically 2, on each side of long thin medial cone (Fig. 10D). Lateral cusps in asymmetrical seriation, migrating from lateral to medial position over 7-8 transverse rows (Fig. 10E). First lateral teeth unicuspidate with cusp towards lateral edge. Second lateral teeth unicuspidate with curved base. Lateral marginal teeth robust and curved. Marginal plates oblong and plain (Fig. 10F).

Male genitalia (Fig. 5A). Terminal organ ('penis') robust and roughly linear with a diverticulum of similar length as the free distal portion. Distorted by spermatophore in holotype (Fig. 5A). Spermatophores (Fig. 5B) short, around half mantle length (22mm, 53.5% of ML in holotype), and thick (1.1mm, 2.7% of ML), produced in low numbers (1 in spermatophore storage sac, 1 in terminal organ in holotype). Oral

cap contains thick coils of ejaculatory apparatus and bears a thick cap thread. Sperm reservoir long, 54% of spermatophore length in holotype, containing a thick sperm cord forming coiled in approximately 24 regular whorl. Only δ specimen is submature. Submature eggs large-type and produced in low numbers (<100). The large eggs indicate that juveniles are likely to adopt a benthic habit on hatching.

Colour in life unknown. Preserved specimens cream with pink-red raised patches scattered on dorsal mantle and upper arm crown. Pink low small papillae on dorsal skin between larger patches. Regular fine papillae on ventral mantle. Dark blue subdermal pigmentation around eyes with superficial red brown chromatophores (Figs 3A, 9C). Webs cream in contrast to pink brown arms. Dorsal White Spots (*sensu* Packard & Sanders, 1971) absent. Scattering of low papillae pronounced around eyes. Lateral mantle ridge present. Small regular low papillae on ventral mantle within lateral ridges.

Nothing known of behaviour or general biology.

DISTRIBUTION. *Octopus bulbus* sp. nov. is known from only 3 specimens, collected off southern Queensland, in 18-195m.

TAXONOMIC REMARKS. *Octopus bulbus* shares a number of attributes with *O. australis* Stranks & Norman, 1993, also found in shallower waters in the region. Both species share a lateral ridge, bulbous ligula and similar gill counts (7-8 in *O. bulbus* versus 7-9 in *O. australis*). However, these taxa have very different floorplans and reproductive characters, suggesting separate evolutionary origins. *Octopus bulbus* has arm and web formulae in which dorsal arms and webs are longer/deeper (AF 1>2>3>4, WF A=B=C>D>E), whereas *O. australis* has longer/deeper lateral arms and webs (AF 3>2>4>1, WF typically D>C>B>E>A). *Octopus bulbus* also has longer arms (4.9-5.6 versus 2.7-4.3 \times ML), shallower webs (10-12% versus 20-30% of longest arm), a proportionally shorter hectocotyliised arm (56% versus 66-86% length of opposite arm) with a higher sucker count (91, 94 versus 62-77), absence of enlarged suckers in mature $\delta\delta$ (suckers 6.7-9.8% versus 12.6-15.3% ML), and spermatophores with far fewer sperm cord whorls (24 versus >60).

The longer dorsal arms (arm formula 1>2>3>4) and a multicuspid radula (2-3 cusps on each side of the rhachidian tooth) are similar to

those of the '*Octopus macropus* group' (Norman, 1993a). However, the gill count of 7-8 is lower than any previously reported for the group all of which possess 10-15 lamellae per demibranch. Until more material becomes available (including fresh tissue for molecular analyses), the higher affinities remain unknown.

***Octopus micros* sp. nov.**
(Figs 6-8, 9D, 10G-H)

MATERIAL. HOLOTYPE: 1♂: 18.8mm ML, MV F87070, east of Mooloolaba, 16-20 miles north of Cape Moreton, southern Queensland, 90-106fm (166-195m), trawl, FV 'Debie-Marie', 11-13 Aug 1981, coll. G. Smith, Queensland Fisheries. Paratypes: 1♂: 20.7mm ML, 1♀: 24.5mm ML, MV F78815, off Mooloolaba, southern Queensland, trawl, FV 'Debie-Marie', 11-13 Aug 1981, coll. G. Smith, Queensland Fisheries (no depth data).

TYPE LOCALITY. East of Mooloolaba, southern Queensland.

ETYMOLOGY. Greek *mikros*, small referring to its small size. 'Pygmy Keeled Octopus' is proposed as a common name.

DIAGNOSIS. Small species (ML to 25mm) with short arms (2-3 × ML) of approximately equal length, dorsal pair slightly shorter. Lateral webs slightly deeper than dorsal web. Enlarged suckers absent in both sexes. Gills with 6 lamellae per demibranch. Hectocotylised arm (third right) approximately 80% of length of opposite arm. Ligula of moderate size (~6% of arm length) with open groove. 85-93 suckers on hectocotylised arm. Terminal organ (penis) robust and linear with simple rounded diverticulum. Spermatophores approximately equal in length with mantle. Lateral mantle ridge present.

DESCRIPTION. Counts and measurements are from the known specimens, 2 mature ♂♂ and a submature ♀ (Table 1).

Robust pygmy species (Fig. 6A); mantle length to 20.7mm for ♂♂, 24.5mm for ♀. Length to 91mm; weight to at least 5.8g. Mantle ovoid to spherical, slightly longer than wide (width 63.3-76.1% of ML), mantle walls moderately muscular. Head width similar to mantle (56.3-76.1% of ML, 89.0-100% of mantle width). Eyes moderate to large and moderately pronounced. Stylets present (Fig. 6B), non-mineralised, 4.4mm in holotype, 23.4% of ML. Mantle aperture of moderate width, approximately half circumference of body at level of opening. Funnel broad and short, approximately one third of mantle length (33.0-41.1% of ML),

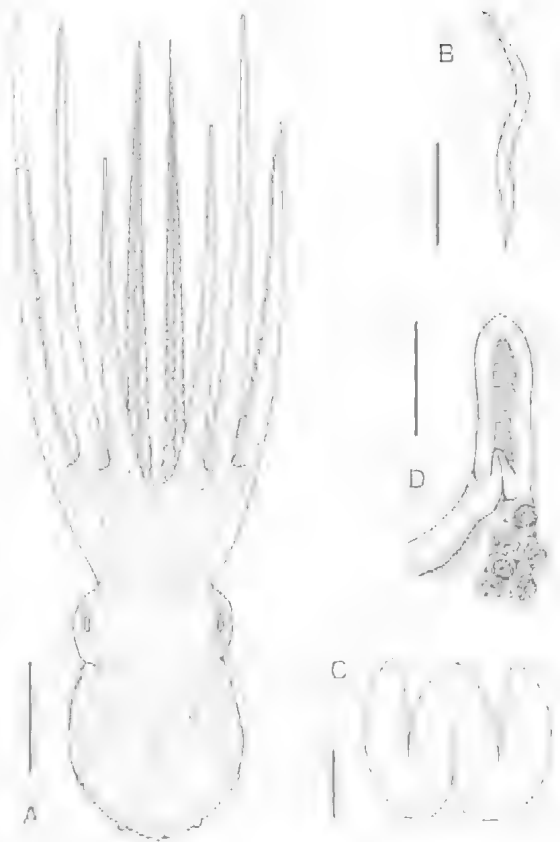


FIG. 6. *Octopus micros* sp. nov. (♂ holotype, MV F87070). A, dorsal view; B, stylet (scale bar = 2mm). C, funnel organ (♀ paratype, MV F78815) (scale bar = 3mm). D, copulatory organ (♂ paratype, MV F78815) (scale bar = 2mm).

free portion 44.7-63.5% of funnel length. Funnel organ W-shaped with broad limbs (Fig. 6C). Outer limbs similar in length to median limbs (outer limbs 92.9-105.2% of median limbs). Funnel organ occupies approximately two thirds of funnel length (60.4-67.7% of funnel length).

Arms of moderate length, longest approximately 2.5 times mantle length (2.3-2.7 × ML). Arms moderately robust relative to mantle length (16.9-19.7% of ML) tapering evenly to fine tips, rounded in cross section. Arms roughly equal in length, dorsal pair slightly shorter (arm formula typically 4=3=2>1). Suckers in 2 rows and of moderate size (9.8-11.7% of ML), slightly elevated with moderate flare and a thin rim. Enlarged suckers absent in both sexes. Approximately 150 suckers on intact arms of mature animals. Webs of moderate depth (deepest web 22.3-27.1% of

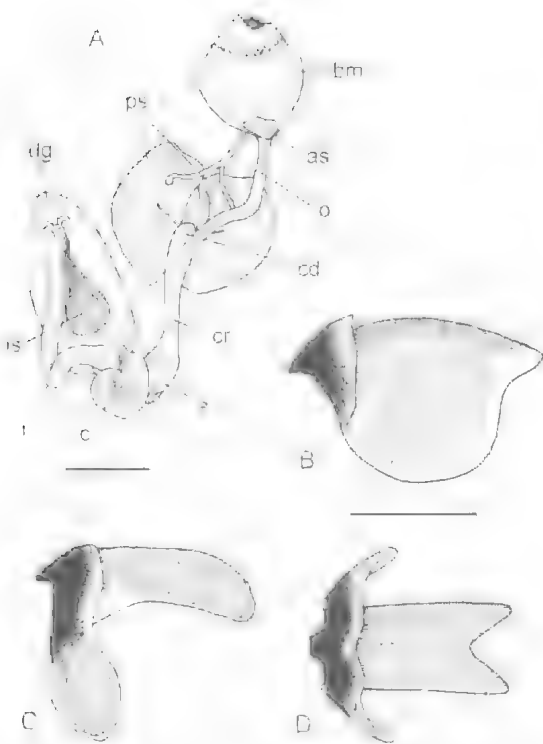


FIG. 7. *Octopus micros* sp. nov. digestive system (♀ paratype, MV F78815); A, digestive tract, symbols as in Fig. 2 (scale bar = 5mm). B-D, beaks (scale bar 3mm); B, upper beak, lateral view; C, lower beak, lateral view; D, lower beak, ventral view.

longest arm). Lateral web sectors slightly deeper than other webs (web formula B=C=D>E>A). Web margins extend as thin ridges for a short distance along ventral edge of arms.

Third right arm of ♂♂ hectocotylised. Modified arm relatively long, almost as long as normal arms ($2.0\text{--}2.2 \times \text{ML}$, 86% of opposite arm in intact male). Ligula moderate-size (6.4% of arm length, 14.4% of mantle length), in the form of an elongate pointed leaf with fine transverse creases across the open ligula groove (Fig. 6D). Calamus distinct and sharp, approximately one half of ligula length (44.4% of ligula). Spermatophore groove well-developed and wide with fine transverse creases. Spermatophore guide shallow with no obvious papillae. 85–93 suckers on hectocotylised arm.

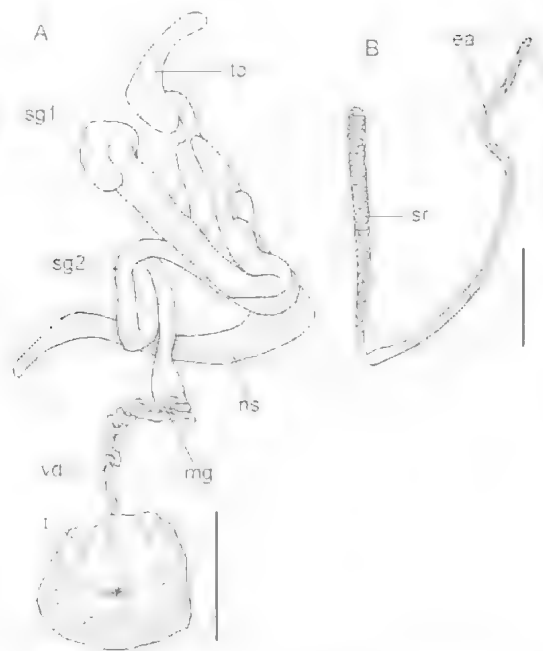
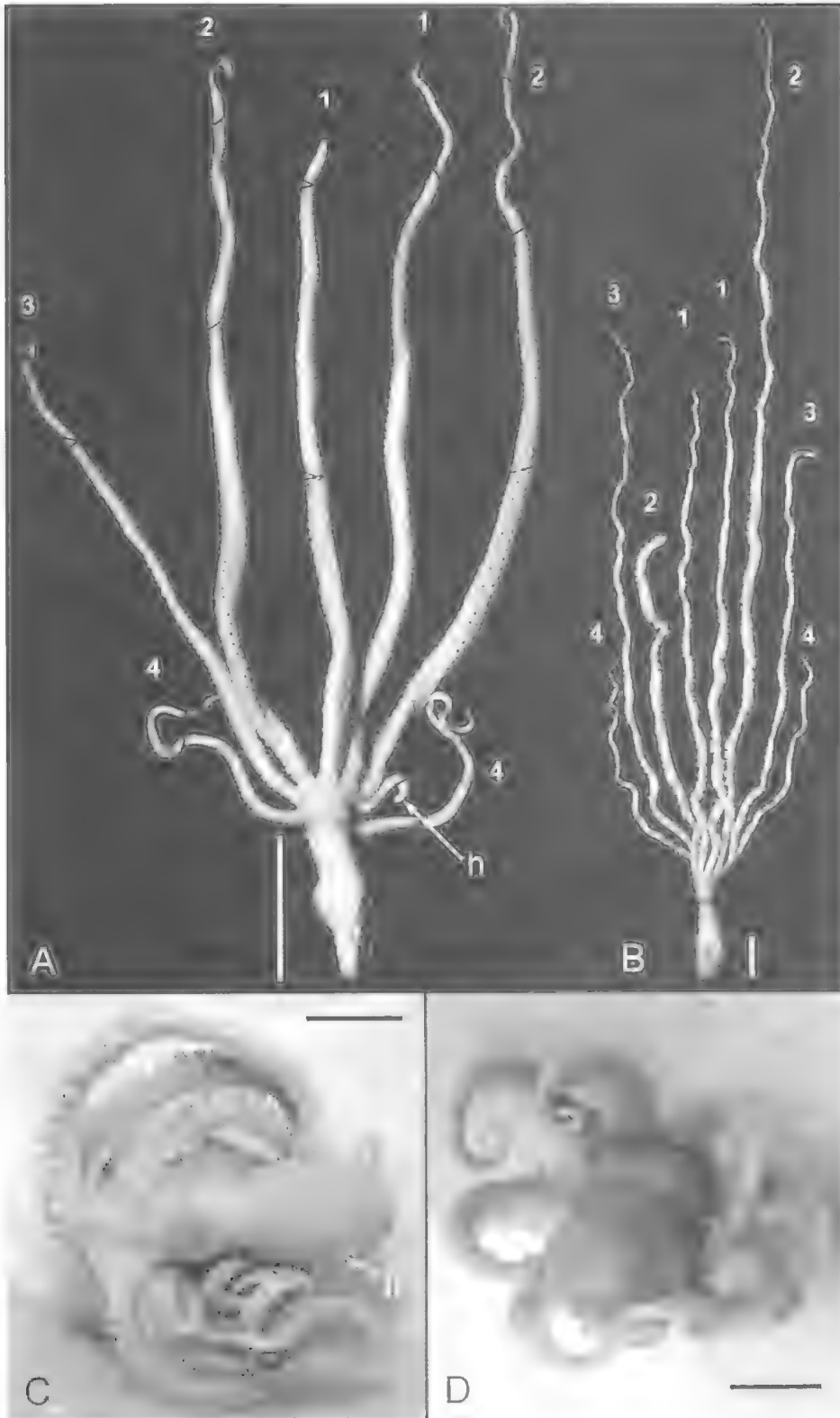


FIG. 8. *Octopus micros* sp. nov. reproductive system (♂ holotype, MV F87070), symbols as in Fig. 5; A, reproductive tract (scale bar = 5mm); B, spermatophore (scale bar = 3mm).

Gills with 6 lamellae on both inner and outer demibranchs, plus terminal lamella.

Digestive tract (Fig. 7A). Anterior salivary glands extend along approximately 20% of buccal mass from posterior margin on dorsal surface. Posterior salivary glands large (slightly longer than buccal mass, approximately 80% of digestive gland length). Crop diverticulum present, small. Stomach bipartite. Caecum coiled in single whorl, with striations. Digestive gland approximately ovoid. Muscular intestine reflexed approximately one third along length from proximal end. Ink sac well developed, embedded in ventral surface of digestive gland. Anal flaps present. Upper beak with slightly hooked rostrum and small hood (Fig. 7B). Lower beak with rounded rostrum, hood narrow, widely spread wings and nearly parallel lateral walls (Fig. 7C–D). Radula with 7 teeth and 2 marginal plates in each transverse row (Fig. 10G–H).

FIG. 9. Type material. A, *Octopus harpedon* sp. nov. (♂ holotype, AM C30411) dorsal view; 1–4: arms numbered from dorsal to ventral pair (scale bar = 50mm). B, *Octopus harpedon* sp. nov. (♀ holotype, AM C30412) dorsal view; 1–4: as in A (scale bar = 50mm). C, *Octopus bulbosus* sp. nov. (♂ holotype, MV F87067), dorso-lateral view; lr = lateral mantle ridge (scale bar = 20mm). D, *Octopus micros* sp. nov. (♂ holotype, MV F87070) dorsal view (scale bar = 10mm).



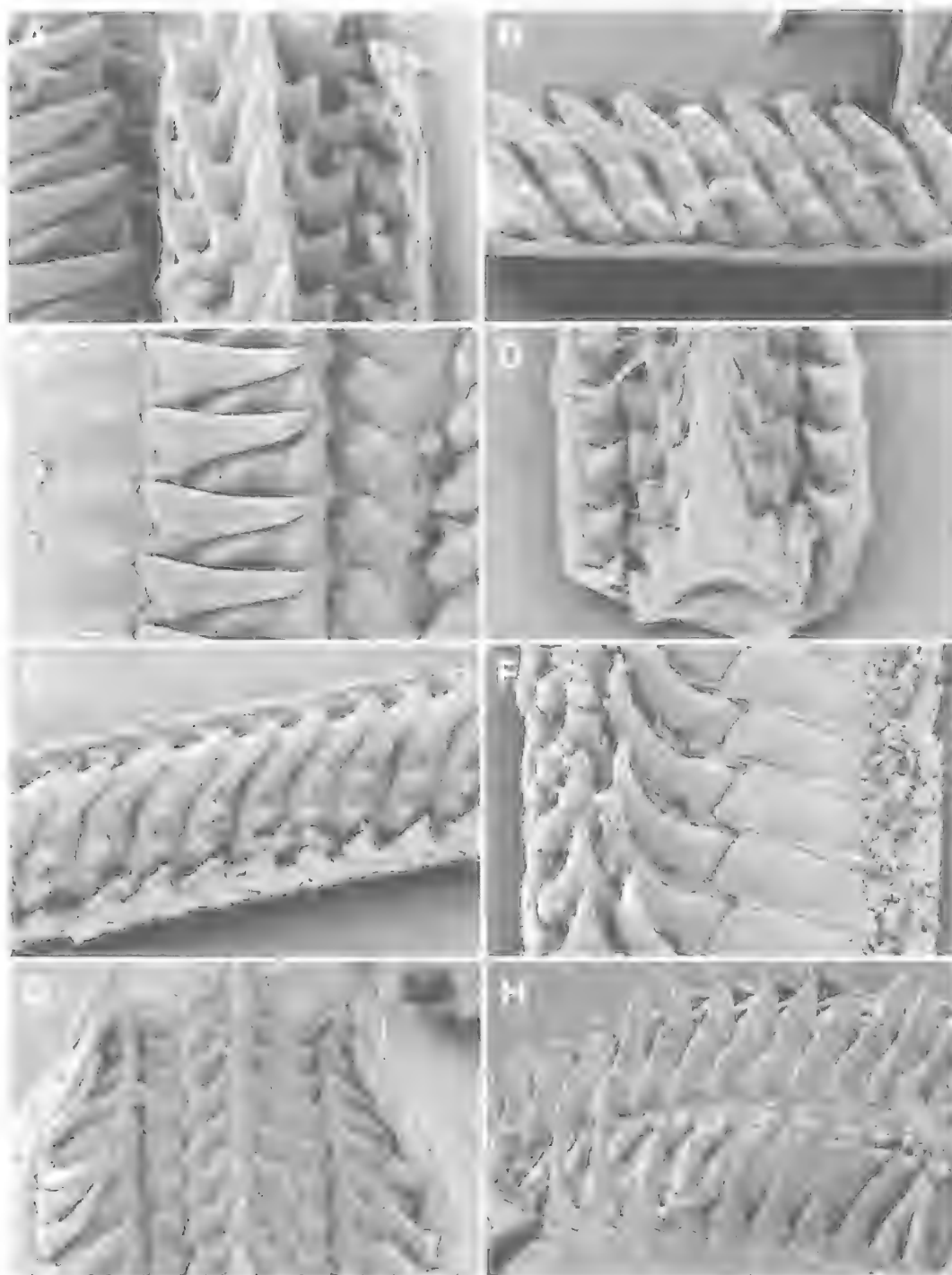


FIG. 10. Radulae. A-C, *Octopus harpedon* sp. nov. radula (♀ paratype, AM C304112). A, dorsal view showing multicuspoid rhachidian tooth; B, lateral view showing serial progression of cusps on rhachidian tooth; C, lateral teeth and marginal plates. D-F, *Octopus bulbus* sp. nov. radula (♀ paratype, MV F87069); D, dorsal view showing multicuspoid rhachidian tooth; E, lateral view showing serial progression of cusps on rhachidian tooth, F, lateral teeth and marginal plates. G-H, *Octopus micros* sp. nov. radula (♀ paratype, MV F78815); G, dorsal view; H, lateral view.

Rhachidian tooth with 1-2 lateral cusps, typically 1, on each side of short robust medial cone (Fig. 10G). Lateral cusps in asymmetrical seriation, migrating from lateral to medial position over 4-5 transverse rows (Fig. 10H). First lateral teeth unicuspidate with cusp towards lateral edge. Second lateral teeth unicuspidate and long with curved base. Lateral marginal teeth long and straight. Marginal plates square, plain (Fig. 10H).

Male genitalia (Fig. 8A). Terminal organ ('penis') in mature ♂ short and robust with simple swollen diverticulum. Spermatophores (Fig. 8B) approximately equal in length with mantle length (20.1, 22.8mm, 97.1, 121.3% ML), and of moderate width (0.5mm [$n=2$], 2.3, 2.5 % of spermatophore length), produced in low numbers (2, 4 in spermatophore storage sac). Ejaculatory apparatus linear with slight coils at oral end. Oral cap simple, bearing long cap thread. Sperm reservoir 37.3% of total spermatophore length in ♂♂, containing robust sperm cord, most of which forms regular whorls with some bunching to produce a plaited appearance.

Submature ♀ with eggs in undeveloped ovary already large (~2mm) and few in number (<100). This species would produce large eggs and the young are likely to be benthic on hatching.

Colour in life unknown. Preserved specimens red-brown formed by fine uniform chromatophores on dorsal surfaces and lateral arm crown to midline of third arm pair. Darker purple-brown pigmentation around eyes creates a 'bruised' appearance to the eyes (Fig. 6A). Dorsal White Spots (*sensu* Packard & Sanders, 1971) present. Skin relatively soft (preservation artefact?) with a single distinct primary papilla over each eye and 4 papillae in a diamond on the dorsal mantle. Large primary papillae on posterior tip of mantle. Lateral mantle ridge present.

Nothing known of behaviour or general biology. Its depth range (>150m) and small size make it unlikely ever to be observed in the wild.

TAXONOMIC REMARKS. *O. micros* sp. nov. is the first pygmy species reported with a lateral mantle ridge. Two other larger species in the area also possess this ridge, *O. bulbosus* described here and *O. australis* Stranks & Norman, 1993. *Octopus micros* is clearly distinguished from *O. bulbosus* by the arm formula ($4=3=2>1$ versus $1>2>3>4$), shorter arms (2.3-2.7 versus 4.9-5.6 \times ML), lower gill count (6 versus 7-8) and the presence of 'dorsal white spots' (*sensu* Packard & Sanders, 1971) and the diamond of primary

papillae on the dorsal mantle (latter two attributes absent in *O. bulbosus*).

O. micros is distinguished from *O. australis* by a higher sucker count on the hectocotyliised arm (85-93 versus 62-77), shorter arms (2.3-2.7 versus 2.7-4.3 \times ML) and a lower gill count (6 versus 7-9). These 2 species share several characters, namely a lateral mantle ridge, similar arm formulae, 'dorsal white spots' and a diamond of primary papillae on the dorsal mantle. These species may share common ancestry.

Only 2 pygmy species have been reported from Australian waters: *O. warringa* Stranks, 1990 and *O. superciliosus* Quoy & Gaimard, 1832 (see Stranks, 1988a). Both are restricted to temperate southern Australian waters. They are easily distinguished from *O. micros* in that they both lack a lateral mantle ridge.

DISCUSSION

Due to the nature of certain marine habitats, our only knowledge of some sea creatures comes from dead material collected by fishing or research trawls. For such animals our capacity to interpret their lives is restricted to deductions based on morphology, stomach contents and habitat associations. The new species described here are all from environments where direct observation is difficult or impossible due to poor water clarity or excessive depths. Combined with the cryptic and/or nocturnal behaviour typical of octopuses, it is likely that none of these species will be observed in their natural environs. Attributes of their morphology, however, may provide some clues to their lifestyles.

O. harpedon is a long-armed species from shallow coastal waters typically clouded with suspended silt over soft sediment substrates. This area is also the regular haunt of abundant tiger sharks and crocodiles, effectively deterring any attempt to find and observe this species *in situ*.

The long arms of *O. harpedon* are similar in scale to those of *Ameloctopus litoralis* Norman, 1992, a small intertidal mudflat species found across northern Australia. *Ameloctopus litoralis* lacks significant webs between the arms and feeds by probing its long and thin arms individually down holes and burrows to capture small crustaceans and fish (Norman, 1992). The long arms and shallow webs of *O. harpedon* suggest that it is similarly using long arms to probe subterranean burrows for crustacean and fish prey. The absence of complex colour patterns

TABLE 1. Counts and measurements (mm) for *O. harpedon*, *O. bulbus* and *O. micros* spp. nov. d = damaged; fr = frozen distorted specimen; H = hectocotyliised arm; InD = indistinct; t = very tip of arm damaged; TO = terminal organ; A-E = web sectors from dorsal sector.

Species	<i>O. harpedon</i>	<i>O. harpedon</i>	<i>O. bulbus</i>	<i>O. bulbus</i>	<i>O. bulbus</i>	<i>O. micros</i>	<i>O. micros</i>	<i>O. micros</i>
Museum	AMS	AMS	MV	MV	MV	MV	MV	MV
Reg. No.	C304111	C304112	F87067	F87068	F87069	F87070	F78815	F78815
Status	Holotype	Paratype	Holotype	Paratype	Paratype	Holotype	Paratype	Paratype
Sex	Male	Female	Male	Male	Female	Male	Male	Female
Maturity	submature	submature	mature	mature	submature	mature	mature	submature
Mantle length	56.9	96.1	41.1	53.0	49.2	18.8	20.7	24.5
Total length	394	997	251	318	67	67	71	91
Weight (g)	45.3	104.3	27.5	47.2	30.1	4.5	4.0	5.8
Mantle width	20.0	23.9	22.0	23d	22d	14.3	13.1	15.5
Head width	15.0	15.2	21.9	17d	22d	14.3	12.3	13.8
Funnel length	29.3	46.0	20.9	33.0	24.3	6.2	8.5	9.6
Free funnel length	7.0	15.4	6.7	13.0	13.6	3.7	3.8	6.1
Funnel organ limb (medial)	InD	InD	12.5	InD	InD	4.2	InD	5.8
Funnel organ limb (lateral)	InD	InD	10.8	InD	InD	3.9	InD	6.1
Shallowest web depth	A: 10	E: 15	E: 18	E: 26	A: 19fr	A: 10	A: 10	A: 10
Deepest web depth	BCE: 13	C: 21	BC: 23	B: 34	D: 30fr	CD: 13	C: 13	C: 14.5
Arm lengths (L/R):	246d 292	543t 591	200 d	d d	275 239d	37 41	39t 43	55 d
2	290d? 334	d 877	171 167	243t 262	233 253	48 50	45 49	d d
3	221 45H	628 495d	106d 82H	240 135H	176 199	39t 42H	48 41H	d d
4	143 148	298t 308t	125 144	187 173	159 d	47 48	47 48	60t 65
Arm width	6.1	5.7	5.7	fr	fr	3.7	3.5	4.5
Sucker diameter	4.0	4.8	3.0	5.2	3.3	2.2	2.3	2.4
Sucker count: R3	49H	d	91H	94H	fr	93H	85H	d
L3	272	291	196 (R4)	fr	fr	156 (R4)	143	153 (R4)
Gill lamellae count: R	10-10	11-10	7-7	8-8	8-8	6-6	6-6	6-7
L	10-10	10-11	7-7	8-8	8-8	6-6	6-6	6-7
Ligula length	3.3	-	6.6	11.6	-	2.7	3.6	-
Calamus length	1.8	-	1.2	2.0	-	1.2	1.3	-
Spermatophore number	-	-	1 (+ 1 in TO)	InD	-	3 (+ 1 in TO)	2	-
Spermatophore length	-	-	22	InD	-	23	20	-
Spermatophore width	-	-	1.1	InD	-	0.6	0.5	-
Sperm reservoir length	-	-	12	InD	-	8.5	7.5	-
Egg number	-	<100	-	-	<100	-	-	<100
Egg length	-	large	-	-	large	-	-	large
Egg width	-	-	-	-	-	-	-	-

and skin sculpture suggest that this species may be nocturnally active.

The other 2 species described here both possess a lateral mantle ridge. This skin structure is only

known in a handful of other described octopods, namely the Australian shallow water *O. australis* Hoyle, 1885 and *O. berrima* Stranks & Norman, 1993, and the deeper water *Benthoctopus leioderma* (Berry, 1911), *Eledone palari* Lu &

Stranks, 1992, *Megaleledone senoi* Taki, 1961 and members of *Bathypolypus* Grinpe, 1921, *Pareledone* Robson, 1932, *Scuturgus* Trosehel, 1857 and *Tetracheledone* Voss, 1955. A partial or broken lateral mantle ridge also occurs in two other shallow water species: *O. himurong* of the '*Octopus macropus* group' (Norman, 1993a) and *O. fungsiuo* of the '*Octopus aegina* group' (Norman, 1993b). Presence of this skin ridge in such disparate taxa suggests either independent origins for this structure or that it is a common primitive state lost in many groups. All the species listed are primarily associated with soft sediment substrates and it is possible that this ridge may relate to their capacity to bury in sand or mud.

Octopus microx is only known from the continental shelf off southern Queensland. This species shows some similarities with *O. australis* and *O. berrima*, from eastern and southern Australia, respectively. All 3 species are unlike any other known shallow-water species and they may represent older Palaeo-austral lineages, the product of the long and isolated northward drift of the Australian continent following the break up of Gondwana around 200 million years ago.

The small size at maturity of *O. microx* is similar to that found in other pygmy species. Such dwarfism appears linked with specialised microhabitats. *O. micropyrus* Berry, 1953 of California (Lang, 1997) and a species from Tasmania (unpubl. data) occur primarily in kelp holdfasts (*Macrocystis* spp.), while *O. hocki* Adam, 1941 of the tropical Indo-West Pacific lives in coral heads (pers. obs.). Juveniles of many octopus species seek refuge in such porous structures (pers. obs.). It is possible that selective pressures against outgrowing the protection of such micro-refuges (and their resident prey species) may have lead to neotenous dwarfism in certain groups. The small size of *O. microx* may reflect a similar specialization for particular microhabitats.

ACKNOWLEDGEMENTS

This research was supported by the Australian Biological Resources Study. Sincere thanks to the following people for assistance with various aspects of this study: Drs Mike Vecchione and Louise Allcock for their constructive comments on the manuscript, David Paul for photography, Joan Clark for SEM, and Ian Loch and Phil Colman (Australian Museum) and Chris Rowley (Museum Victoria) for curatorial assistance.

LITERATURE CITED

- DONCE, Z. 1987. Fauna Sinica. Phylum Mollusca, class Cephalopoda. (Science Press: Beijing, China).
- NORMAN, M.D. 1992. *Amelotopus litoralis* gen. & sp. nov. (Cephalopoda: Octopodidae), a new shallow-water octopus from tropical Australian waters. *Invertebrate Taxonomy* 6: 567-582.
- 1993a. Four new species of the *Octopus macropus* group (Cephalopoda: Octopodidae) from the Great Barrier Reef Australia. *Memoirs of the Museum of Victoria* 53(2): 267-308.
- 1993b. Ocellate octopuses (Cephalopoda: Octopodidae) of the Great Barrier Reef, Australia: description of two new species and redescription of *Octopus polyzema* Gray, 1849. *Memoirs of Museum of Victoria* 53(2): 309-344.
- 1993c. Systematics and biogeography of the shallow-water octopuses (Cephalopoda: Octopodidae) of the Great Barrier Reef, Australia. Unpubl. PhD thesis, University of Melbourne.
- 1993d. *Octopus ornatus* Gould, 1852 (Cephalopoda: Octopodidae) in Australian waters: morphology, distribution and life history. *Proceedings of the Biological Society of Washington* 106(4): 645-660.
1998. Family Octopodidae. Benthic octopuses. Pp. 800-826. In Carpenter, K.E. & Niem, V.H. (eds) *FAO Species Identification Guide for fishery purposes. The living marine resources of the Western Central Pacific*. Vol. 2. (FAO: Rome).
- NORMAN, M.D. & FINN, J. 2001. Revision of the *Octopus horridus* species group with description of two member species from the Great Barrier Reef, Australia. *Invertebrate Taxonomy* 15: 13-35.
- NORMAN, M.D. & HOCHBERG, E.G. 1994. Shallow-water octopuses (Cephalopoda: Octopodidae) of Hong Kong territorial waters. Pp. 141-160. In Morton, B. (ed.) *The Malacofauna of Hong Kong and southern China III, Proceedings of the Third International Workshop on the Malacofauna of Hong Kong and southern China* (Hong Kong University Press: Hong Kong).
- NORMAN, M.D., E.G. HOCHBERG & LU, C.C. 1997. Mollusca Cephalopoda: Mid-depth octopuses (200-1000 m) of the Banda and Arafura Seas (Octopodidae and Alloposidae). *Bulletin de Museum National d'Histoire Naturelle, Paris* 172: 357-383.
- PACKARD, A. & SANDERS, G.D. 1971. Body patterns of *Octopus vulgaris* and maturation of the response to disturbance. *Animal Behavior* 19: 780-90.
- STRANKS, J.N. 1988a. Systematics of the family Octopodidae (Mollusca: Cephalopoda) of south-eastern Australia. Unpubl. MSc thesis, University of Melbourne, Victoria.
- 1988b. Redescription of *Octopus pallidus* (Cephalopoda: Octopodidae) from south-eastern Australia. *Malacologia* 29(1): 275-287.
1990. Three new species of *Octopus* (Mollusca: Cephalopoda) from south-eastern Australia.

- Memoirs of the Museum of Victoria 50(2): 457-465.
- STRANKS, T. & NORMAN, M.D. 1993. Review of the *Octopus australis* complex (Cephalopoda: Octopodidae) and description of a new species. Memoirs of the Museum of Victoria 53(2): 345-373.
- VOSS, G.L. 1971. Cephalopods collected by the R/V John Elliott Pillsbury in the Gulf of Panama in 1967. Bulletin of Marine Science 21(1): 1-34.
1975. *Euaxoctopus pillsburyae*, new species, (Mollusca: Cephalopoda) from the southern Caribbean and Surinam. Bulletin of Marine Science 25(3): 346-352.
- VOSS, G.L. & WILLIAMSON, G.R. 1972. Cephalopods of Hong Kong. (Hong Kong Government Press: Hong Kong).

HALACARIDAE FROM THE GREAT BARRIER REEF LAGOON AND CORAL SEA: *HALACARELLUS* AND *HALACARUS* (ACARINA: HALACAROIDEA)

Otto, J.C. 2001 06 30: Halacaridae from the Great Barrier Reef lagoon and Coral Sea: *Halacarellus* and *Halacarus* (Acarina: Halacaroidea). *Memoirs of the Queensland Museum* 46(2): 691-716. Brisbane. ISSN 0079-8835.

The marine mites *Halacarellus* and *Halacarus* are recorded for the first time from northeastern Australia. *Halacarellus katewilsonae* sp. nov. and seven new species of *Halacarus*, namely *chilcottensis*, *heraldensis*, *juliani*, *sabulonis*, *rarus*, *striolus* and *tritoni* are described. *Halacarus rarus* belongs to the *ctenopus* group, *H. tritoni* to the *actenos* group and the other five new *Halacarus* species to a newly proposed *membraneus* group. *Halacarus discophorus* Bartsch, a species previously described from southwestern Australia, is recorded from northwestern and northeastern parts of the continent. A key to Australian species of *Halacarus* and *Halacarellus* is presented. □ *Halacarids*, *Halacarellus*, *Halacarus*, Great Barrier Reef, Australia, Coral Sea, Queensland Plateau.

Jürgen C. Otto, Australian Institute of Marine Science, PMB 3, Townsville 4810 (e-mail: j.otto@aims.gov.au), Australia; 4 July 2000.

This paper is one in a series describing mites in the predominantly marine Halacaridae, that were found during a survey on the Great Barrier Reef and reefs in the Coral Sea. Bartsch (2000), Otto (1999a-c, 2000a-i) and Otto & Bartsch (2000) dealt with 19 genera and this paper describes species of *Halacarellus* and *Halacarus*.

Halacarellus lubricus Bartsch and *Halacarus oblongus* Lohmann are known from SE Australia (Lohmann, 1893; Otto, 1994), and 12 species occur in SW Australia (Bartsch, 1993a, 1999a). This paper provides first records of *Halacarellus* and *Halacarus* from tropical Australia.

METHODS

All material was collected by the author except where stated otherwise. Mites were cleared in lactic acid and mounted in PVA. Drawings were made with the aid of a camera lucida. In the figure legends, letters enclosed by parentheses refer to illustrations that do not have scale bars but are drawn to the same magnification as those referred to by the letter that precedes the parentheses. In the accounts of each species only one sex is described in detail; for the opposite sex only characters that differ are described. Measurements or counts given as ranges are based on all available material. In the accounts of leg chaetotaxy, numbers enclosed in parentheses refer to rare setal complements. Abbreviations in descriptions: AD, anterior dorsal plate; AE, anterior epimeral plate; glp-1 to glp-5, dorsal gland pores numbered from anterior to posterior; ds-1 to ds-6, dorsal idiosomal setae (excluding those on posterior epimeral plate) numbered in sequence from anterior to posterior; GA,

genitoanal plate; GO, genital opening; OC, ocular plate; pas, parambulacral seta(e); pgs, perigenital seta(e); PD, posterior dorsal plate; PE, posterior epimeral plate; P-1 to P-4, palp segments numbered in sequence from base of palp; sgs, subgenital seta(e); leg I to leg IV. Specimens with the registration number prefix QMS are deposited in the Queensland Museum. Other depositories for type or non-type material are: AIMS, Australian Institute of Marine Science, Townsville; ANIC, Australian National Insect Collection, Canberra; ZMH, Zoologisches Museum der Universität Hamburg, Germany.

SYSTEMATICS

Superfamily HALACAROIDEA Cunliffe, 1955
Family HALACARIDAE Murray, 1877
***Halacarellus* Viets, 1927**

Halacarellus Viets, 1927: 120. Bartsch, 1997: 1223; 1998: 150.

Thalassarachna Packard, 1871, sensu Newell, 1945: 59 (in part; see Bartsch, 1997). Newell, 1984: 89. Green & Macquitty 1987: 116. Otto, 1994: 40.

TYPE SPECIES. *Halacarus balticus* Lohmann, 1889, by original designation.

DIAGNOSIS. Idiosoma with AD, OC and PD, 6 pairs of dorsal idiosomatic setae and up to 5 pairs of gland pores. No setae within ventral membranous cuticle. Palps 4-segmented. P-2 with 1 seta. P-3 with a medial spur or seta. P-4 with 3 setae in basal whorl. Genua shorter than telofemora and tibiae. All tarsi with 3 dorsal setae. Tarsus I with several eupathidia apically and 1 non-eupathid ventromedial seta (only exception with 2 such setae: *H. procerus*). Solenidion on tarsus I dorsolateral, on tarsus II dorsomedial.

REMARKS. Newell (1945, 1984), Green & MacQuitty (1987) and Otto (1994) regarded *Halacarellus* as a junior synonym of *Thalassarachna* Packard, following Newell's (1945) argument that their type species (*H. balticus* and *T. verrillii*) are congeners. However, Bartsch (1972, 1990) rejected Newell's proposal on the basis that *T. verrilli* is insufficiently known and its affinities with *Halacarellus* not well proven. As a result, *Thalassarachna* and *Halacarellus* were used in parallel for the same genus over several decades. Bartsch (1997) argued that *Halacarellus* sensu Viets (= *Thalassarachna* sensu Newell) consists of 2 subgroups, one containing the *Halacarellus* type, *Halacarus balticus*, and the other with the *Thalassarachna* type, *T. verrillii* (= *Acarus basteri* Johnston). Hence, *Halacarellus* sensu Viets was split into *Halacarellus* s. str. and *Thalassarachna* s. str. as used herein.

***Halacarellus katewilsonae* sp. nov.**
(Figs 1,2)

ETYMOLOGY. For Kate Wilson, for her continuous support.

MATERIAL. HOLOTYPE: QMS105569, 1 ♂, Queensland Plateau, Chilcott Islet, 16°56.611'S 150°0.177'E, 14 Sep. 1998, coarse sand at 0.5m. PARATYPES: Queensland Plateau: QMS105570-105573, 4 ♂, QMS105574-105577, 4 ♀, ZMH. 1 ♂, ANIC, 1 ♂, data as for holotype; QMS105578/105579, 2 ♂, South Willis Islet, ca. 16°18'S 149°58'E, 15 Sep. 1998, coral rubble at 0-10m; QMS105580, 1 ♂, Herald Cays, 16°57.171'S 149°12.036'E, coarse sand at 5-15m.

DESCRIPTION. *Male*. Idiosoma. 394-444µm long (holotype 441µm). All idiosomal plates finely punctate; other ornamentation absent, except for a series of pits on AD, OC and PD (Fig. 1A). AD longer than wide; truncated or rounded posteriorly; with glp-1 and pair of ds-1. Setae ds-2, ds-3 and ds-4 inserted in finely striated membranous cuticle. OC similar in length to AD; at least 3 times longer than wide and slightly curved; two pores, one anteriorly, the other posteriorly; pore canaliculus near posterior margin. PD shorter than half of idiosoma; strongly convex anteriorly; pair of ds-5 in anterior half, pair of glp-4 posteriorly. Ventrally with pair of oblong subcuticular sclerites between AE and PE (Fig. 1B). PE with one dorsal and 3 ventral setae. GA with ca. 24-32 pgs surrounding GO, one pair slightly offset anteriorly (Fig. 1C); 4 pairs of sgs seen, the 3 posterior pairs more difficult to discern than the anterior pair. Posterolaterally to GO a pair of lyrifissures.

Gnathosomal base slightly wider than long and about as long as rostrum (Fig. 1E); one pair of maxillary setae inserted at level of palp insertions, the other more delicate pair in anterior half of rostrum; two pairs of rostral setae near tip of rostrum. Pharyngeal plate with 4 pairs of panels. Segment P-3 with spur.

Lateral flanks of legs finely punctate, more conspicuously on telofemora than on other segments. Chaetotaxy (trochanter-tibia): I 1-2-4-5-13 (Fig. 2A), II 1-2-5-5-9 (Fig. 2D), III 2-3-3-3-6 (Fig. 2E), IV 0-3-3-3-6 (Fig. 2F). Ventral setae on tibia I slightly thickened basally but not distinctly spiniform. Tibia II with 2 and tibiae III and IV each with 3 bipectinate setae; those on tibia IV shorter, less conspicuously pectinate than others. Telofemur IV with short dorsal spine. Tarsus I with 3 dorsal setae, solenidion, ventromedial seta and 7-9 pairs of eupathid pas (Fig. 2B,C). Tarsus II with 3 dorsal setae (distomedial 1 closer to most proximal than to distolateral 1), solenidion, 1 ventral seta, and pair of doubled pas. Tarsi III and IV with 3 dorsal setae (both distal ones at similar distance from proximal margin of segment) and pair of pas-singlets. Paired claws of tarsus I with barely visible pecten, those on other tarsi much more distinctly pectinate. All paired claws with accessory process.

Female. Idiosoma 386-459µm long. GA with 3 pairs pgs, but no sgs (Fig. 1D).

REMARKS. Other *Halacarellus* that have an elongate OC with one gland pore anteriorly and one posteriorly, a pair of maxillary setae in distal third of rostrum and the other pair level with the palp insertions, 3 ventral setae on tibiae III and IV, and 2, 2, 3 and 3 setae on basifemora I-IV, respectively, are those in the *H. harti* group (Bartsch, 1997, 1999a), *harti* (Trouessart, 1889), *kerquensis* (Lohmann, 1907), *lubricus* Bartsch, 1985, *porcellus* Bartsch & Pugh, 1994 and *rotnestensis* Bartsch, 1999a. *H. katewilsonae* differs from these by the OC being distinctly more elongate and by the dorsal plates lacking costae, areolae or reticulation.

An OC similar in shape to that of *H. katewilsonae* occurs in *Peregrinacarus reticulatus* Bartsch, a species closely related to *Halacarellus* (Bartsch, 1999b). *Halacarellus* differs from *Peregrinacarus* by its medioventral seta on tarsus I.

Of 46 known species of *Halacarellus* (Bartsch, 1997, 1998, 1999a), *H. katewilsonae* becomes the third tropical one, with *H. vajetus* from Tanzania (Bartsch, 1974) and *H. tropicalis* from Venezuela (Bartsch, 1984).

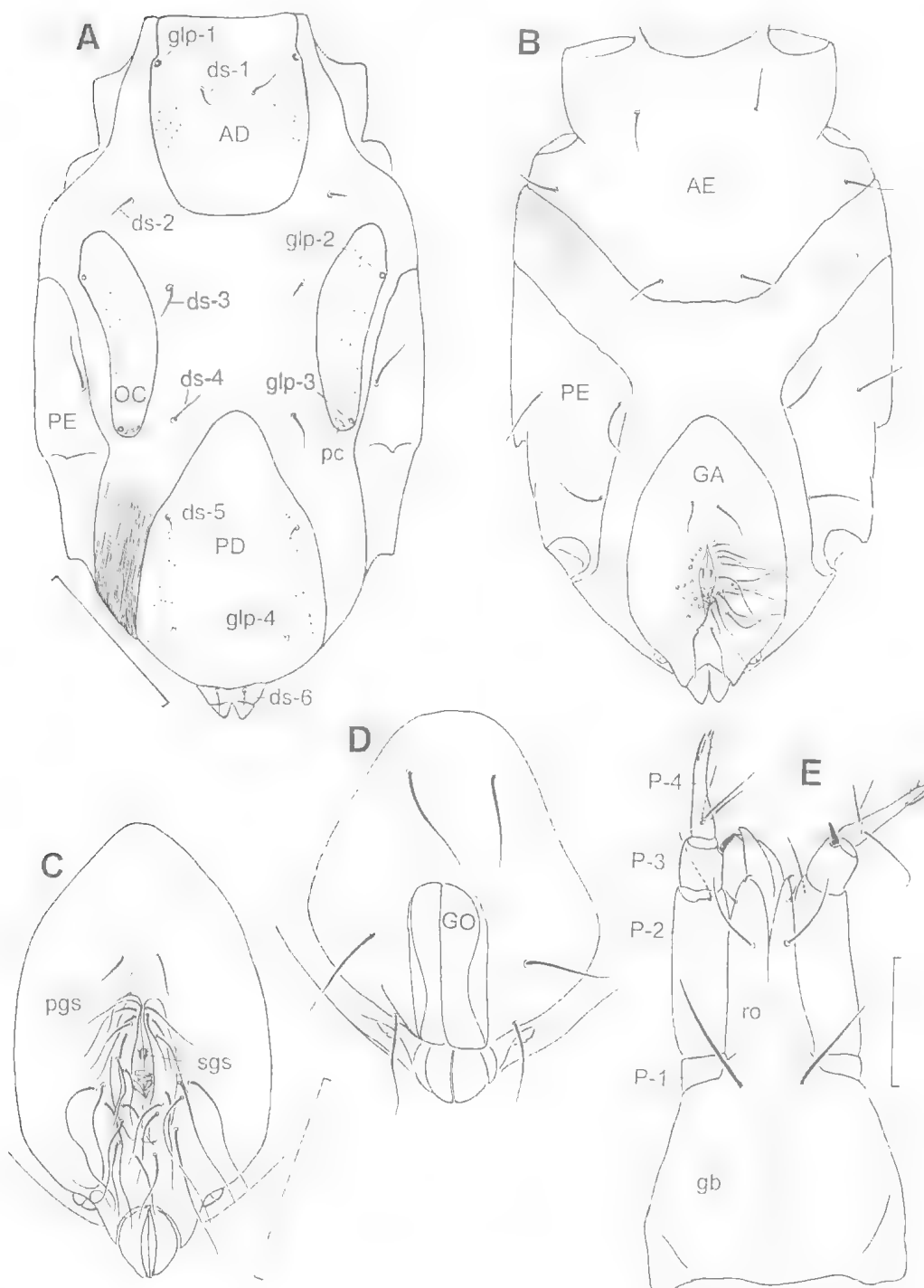


FIG. 1. *Halacarellus katewilsonae* sp. nov., adult. A, ♂, idiosoma, dorsal view; B, ♂, idiosoma, ventral view; C, ♂, genitoanal plate; D, ♀, genitoanal plate; E, ♂, gnathosoma, ventral view; AD, anterior dorsal plate; AE, anterior epimeral plate; ds-1 to ds-6, dorsal setae; GA, genitoanal plate; gb, gnathosomal base; glp-1 to glp-4, gland pores; GO, genital opening; PD, posterior dorsal plate; PE, posterior epimeral plate; pc, pore canaliculus; pgs, perigenital setae; sgs, subgenital setae. P-1 to P-4, palp segments; ro, rostrum. Scale bars: A (B) = 100 µm; C (D), E = 50 µm.

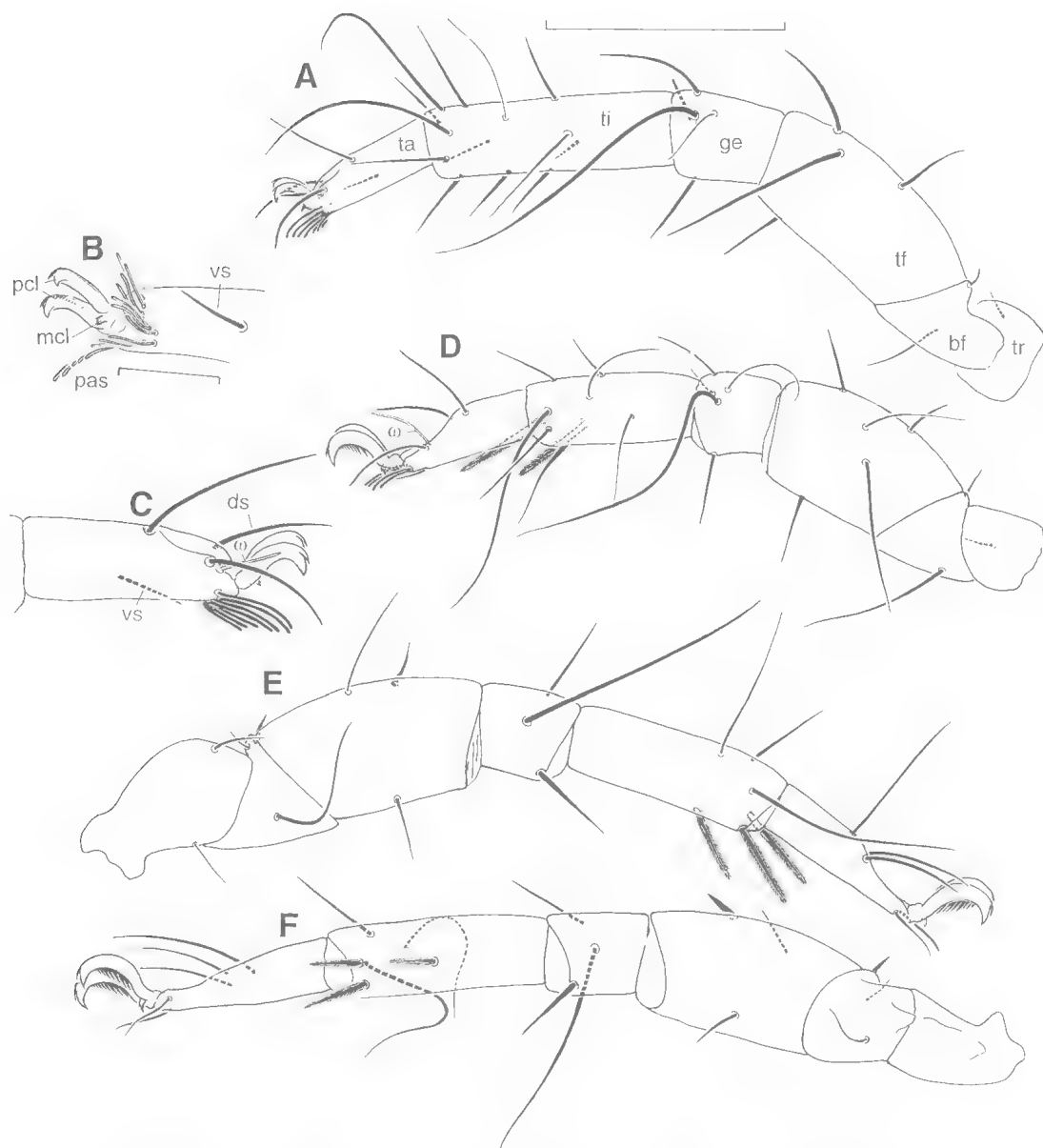


FIG. 2. *Halacarellus katewilsonae* sp. nov., adult. A, ♂, leg I, dorsolateral view; B, ♂, tarsus I, ventromedial view; C, ♂, tarsus I, lateral view (medial eupathidia omitted); D, ♂, leg II, lateral view; E, ♂, leg III, lateral view; F, ♀, leg IV, ventral view. bf, basifemur; ds, dorsal setae on tarsus; ge, genu; mcl, median claw; pas, parambulacral setae; pcl, paired claws; ta, tarsus; ti, tibia; tr, trochanter; vs, ventral seta on tarsus; w, solenidion. Scale bars: B (C) = 25µm; A (D, E, F) = 100µm.

Halacarus Gosse, 1855

Halacarus Gosse, 1855: 27. Bartsch, 1983: 181; 1993a: 46; 1993c: 22. Green & MacQuitty, 1987: 110. Newell, 1984: 37.

TYPE SPECIES. *Halacarus ctenopus* Gosse, 1855; by monotypy.

DIAGNOSIS. AD often with frontal spine. OC and PD present or absent. PD, if present, in ♂♂ often larger than in ♀♀. Most species with 5 pairs of distinct gland pores. Posteriormost dorsal seta (ds-6) inserted close to posterior pair of gland pores (glp-5). Both pairs of maxillary

setae on rostrum. Palps inserted laterally; P-2 with 2 setae, P-3 with medial spine; P-4 with 3 basal setae. Leg I stronger than other legs, with smooth or apically pectinate spines on tibia, genu and telofemur. Genu almost as long as telofemur or tibia. Solenidion dorsolateral on tarsus I, dorsomedial on tarsus II. Tarsus I with setiform famulus.

***Halacarus chilcottensis* sp. nov.**
(Figs 3-5)

ETYMOLOGY. From Chilcott Islet.

MATERIAL. HOLOTYPE: QMS105619, ♂, Queensland Plateau, Chilcott Islet, 16°56.51'S 150°0.4E', 14 Sep. 1998, G.A. Diaz-Pulido, coarse sand at 10-15m. PARATYPE: QMS105620, 1 ♂, ZMH, 1 ♂, data as for holotype.

DESCRIPTION. *Male*. Idiosoma 599-604 µm long (holotype 599 µm). Dorsal plates covered by striated epicuticle (Fig. 4F). Membranous cuticle between plates as in Fig. 4G. AD drawn out anteriorly into a stout frontal spine (Fig. 3A); with pair of glp-1 and pair of ds-1. Setae ds-2, ds-3 and ds-4 in membranous cuticle. Pores glp-2 (Fig. 3B), glp-3 and glp-4 on platelets in membranous cuticle (Fig. 3A). OC separated from glp-3; variable in shape between and within specimens (Fig. 4A-C); lacking cornea but with pore canaliculus laterally. Posterior to glp-3 pair of plates that vary in shape. Setae ds-5 inserted on PD (Fig. 3D), except for one side in one specimen where it inserts in membranous cuticle (Fig. 3A). PD with variable and uneven anterior margin (Fig. 3D); posterior half with a series of minute pits underneath epicuticle; glp-5 situated on posterior swellings. Three pairs of setae on AE, 4 setae on PE, no setae in membranous ventral cuticle (Fig. 3C). Epicuticle on AE with fingerprint-like striation pattern (Fig. 4H). GA with two pairs of outlying pgs and ca. 29 pgs closely surrounding GO. Sgs not clearly seen.

Rostrum about as long as gnathosomal base; with one pair of maxillary setae in proximal half, the other pair in distal half (Fig. 4E). Palp transversely striated; both setae on P-2 inserted distally; P-3 with tapering but apically blunt spine (Fig. 4D).

All leg segments finely striated (Fig. 5B). Leg chaetotaxy (trochanter - tibia): I 1-2-7-8-15 (Fig. 5A), II 1-3-7-8-12 (11,13) (Fig. 5D), III 2-3(2)-5-6-9 (Fig. 5F), IV 1-2-4-6-10 (Fig. 5H). Telofemur and genu I with two, tibia I with 4 heavy ventral or ventromedial spines; less heavy spines on most other leg segments, including one

dorsally on all basifemora, a set of usually 3, sometimes 4 (Fig. 5D), dorsally on tibia II, two dorsally on genu II, and two dorsally on telofemur II. Tarsus I with 3 dorsal setae, two pairs of ventral setae (the distal ones eupathidia), and pair of doubled pas; solenidion and famulus closely associated and of similar length and thickness (Fig. 5C). Tarsus II with 3 dorsal setae, pair of ventral setae, pair of doubled pas and solenidion (Fig. 5E). Tarsus III with 4 dorsal setae, one doubled pas, one pas singlet, and pair of ventral setae (Fig. 5G). Tarsus IV with 3 dorsal setae, pair of ventral setae, and pair of plumose pas singlets (Fig. 5I). Paired claws of legs I and IV smooth, of tarsi II and III with conspicuous pecten. Empodial claws not seen.

Female. Unknown.

REMARKS. *H. chilcottensis* belongs to the *membraneus* group. Members of this group have well-developed OC and PD, a pair of platelets immediately posterior to the OC, finely reticulated epicuticle on all plates, AD developed into a short, robust spine, 4 spines on telofemur I. Other species in group are *H. membraneus* Bartsch, 1981, and 4 new species (*heraldensis*, *sabulonis*, *juliani* and *striolus*). *H. chilcottensis* differs from these, among other characters, in its 3 or 4 spines dorsally on tibia II. In other species the dorsal setae on that segment are not distinctly spine-like or thickened.

A species closely related to the *membraneus* group is *Halacarus parmatus* Bartsch, 1993c, from Antarctica. It too has platelets posterior to the ocular plate and a similar AD. However, it is not included here as it differs, amongst other characters, in having 1 seta inserted proximally on P-2, and only 2 spines on telofemur I.

***Halacarus discophorus* Bartsch, 1993a**
(Fig. 6)

MATERIAL. GBR Marine Park: QMS105581-105610, 11 ♀, 19 ♂, ANIC, 1 ♀, 1 ♂, AIMS, 15 ♂, 7 ♀, ZMH A83/00, 1 ♂, 1 ♀, Pandora Reef, 18°49'S 146°26'E, Elizabeth Reef, 19°20.12'S 149°02.85'E, Faraday Reef, 18°25.93'S 147°21.11'E, Myrmidon Reef, 18°16.69'S 147°23.21'E, Club 21 Reef, 19°22.36'S 149°01.05'E, Loadstone Reef, 18°41.29'S 147°05.83'E and 18°42.05' 147°05.98'E, Turner Cay, ca. 21°43'S 152°33'E, Great Palm Island, 18°40.60'S 146°34.29'E and 18°40.98'S 146°35.19'E, Sand Bank No. 1, 14°18'S 145°12'E, Chinaman Reef, ca. 22°00'S 152°40'E, Lizard Island, Boulder Reef, ca. 15°24'S 145°27'E, Yonge Reef, ca. 14°36'S 145°38'E, Rosser Reef, ca. 15°37'S 145°33'E, Reef 14-056, 14°19.5'S 144°57.5'E, Lavers Cay, 21°13'S 151°59'E, East Cay, 21°29'S 152°33'E; Reef 21-433, 21°33'S 151°28.5'E, Reef 21-551, 21°57.54'S

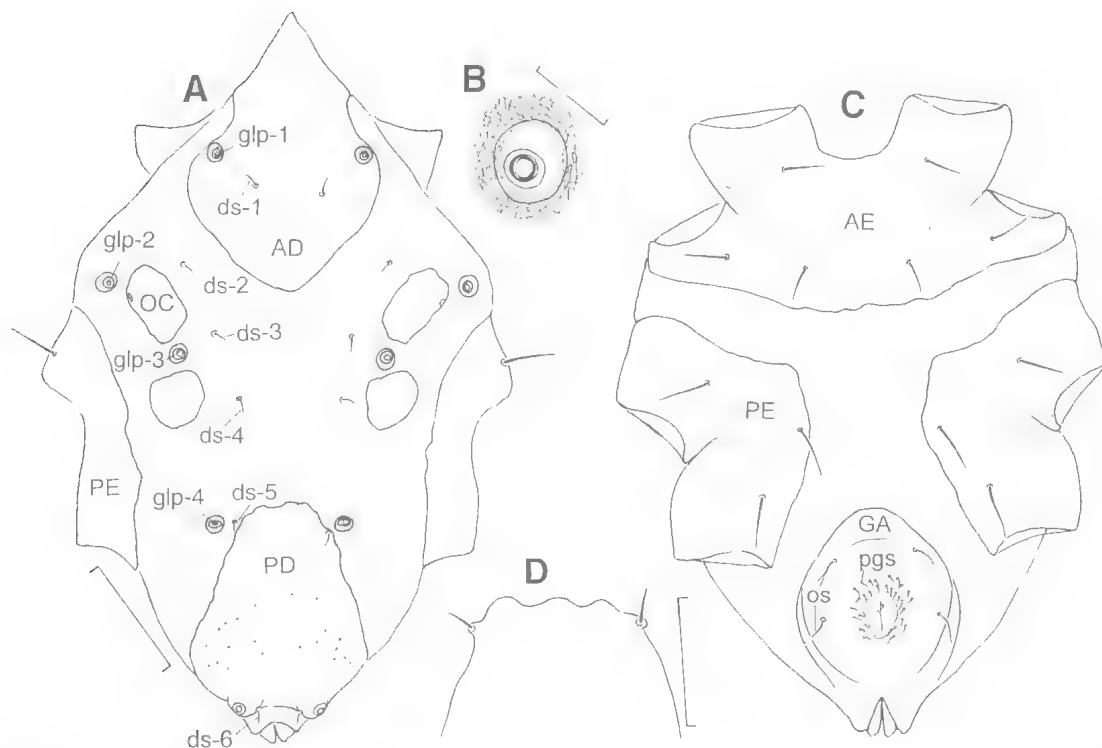


FIG. 3. *Halacarus chilcottensis* sp. nov., ♂. A, idiosoma, dorsal view; B, gland pore 2; C, idiosoma, ventral view; D, anterior part of PD. AD, anterior dorsal plate; AE, anterior epimeral plate; ds-1 to ds-6, dorsal setae; GA, genitoanal plate; glp-1 to glp-4, gland pores; OC, ocular plate; os, outlying perigenital setae; PE, posterior epimeral plate; PD, posterior dorsal plate; pgs, perigenital setae. Scale bars: A (C) = 100 μ m; B = 20 μ m; D = 50 μ m.

152°04.60'E, Reef 21-149, 21°06'S 151°43'E, 22 Apr. 1999, coarse sand at 0.5m, Reef 22-088, 22°01.5'S 152°09'E. Queensland Plateau: QMS105611-105613, 2 ♂, 1 ♀, Chilcott Islet, 16°56.611'S 150°0.177'E & 16°56.51'S 150°0.4'E. Western Australia: WAM, 1 ♂, off Montebello Islands, 20°22.12'S 115°31'E. All material was collected in mostly coarse sediment at 1-17m depth.

REMARKS. These specimens are first records of the species from NE and NW Australia. The only previous records were from the type locality on Rottne Island, WA (Bartsch, 1993a).

H. discophorus is characterised by a PD, the insertion of ds-5 and ds-6 on the same sclerites as glp-4 and glp-5, respectively (Fig. 6A), and a pair of plates between glp-4 and glp-5 in the male (Fig. 6A). It can be further distinguished from similar species (e.g. *H. flavellus* Bartsch, 1993a) by having only one side of the spinose setae on tibia II pectinate (Fig. 6B) instead of both sides.

Males from the Great Barrier Reef, measuring 502-578 μ m, are slightly smaller than the type from Rottne Island (610 μ m) or the two males from the Queensland Plateau (586 μ m and

641 μ m); the specimen from the Montebello Islands in Western Australia is even smaller (470 μ m). However, no other differences were detected and these specimens are therefore regarded as conspecific.

***Halacarus heraldensis* sp. nov.** (Figs 7-9)

ETYMOLOGY. From the type locality.

MATERIAL: HOLOTYPE: QMS105621, ♂, Queensland Plateau, Herald Cays, 16°57.171'S 149°12.036'E, 16 Sep. 1998, G.A. Diaz-Pulido, coarse sand at 5-15m. PARATYPES: QMS105622, 1 ♂, QMS105623, 1 ♀, ANIC, 1 ♂, ZMH A76/00, 1 ♂, data as for holotype.

DESCRIPTION. *Male.* Idiosoma 386-417 μ m long (holotype 386 μ m). Dorsal plates covered by epicuticle structured (Fig. 7B), but PD with such epicuticle only anteriorly and laterally, remainder finely punctate (Fig. 7E). Membranous cuticle between plates (Fig. 7D). AD drawn out anteriorly into a short frontal spine (Fig. 7A); posterior margin broadly convex; with

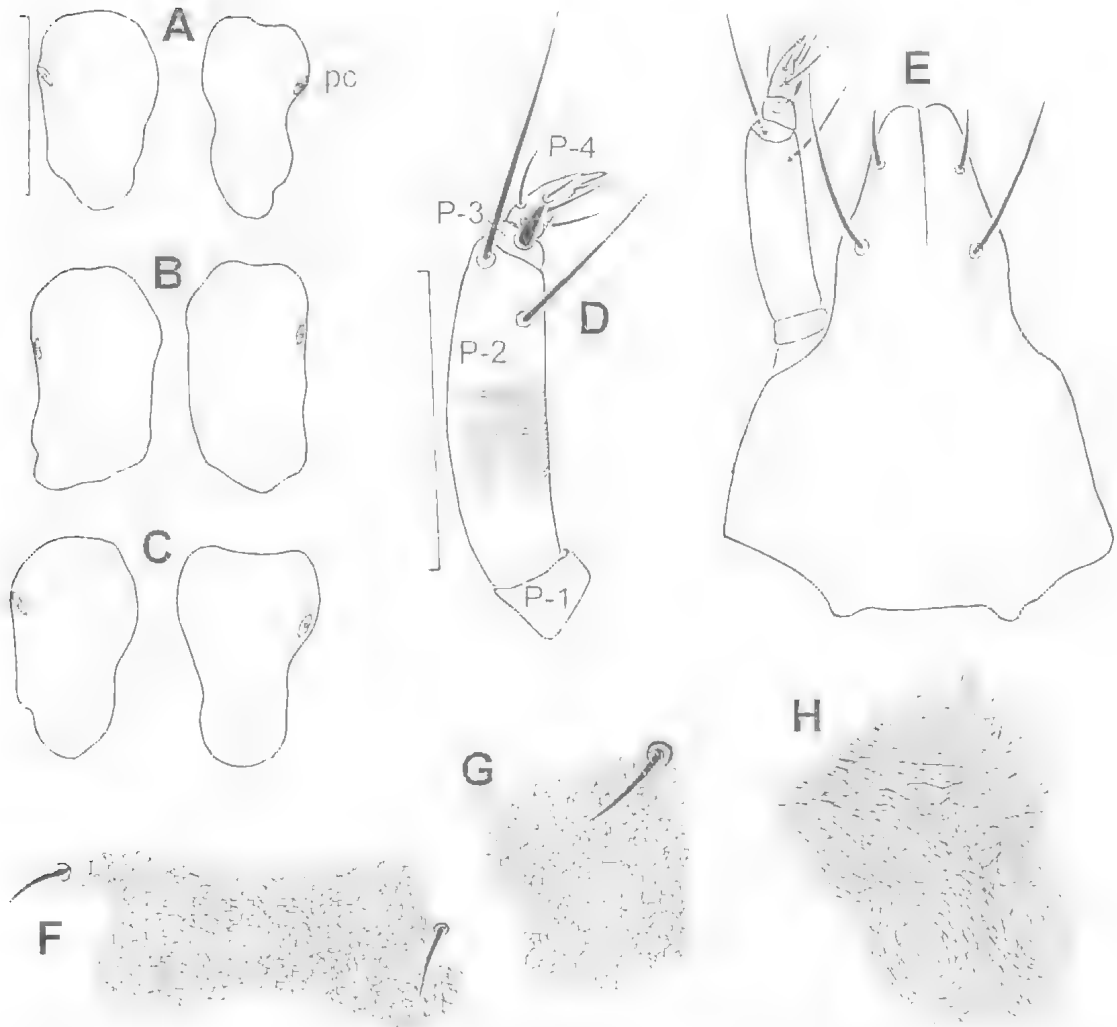


FIG. 4. *Halacarus chilcottensis* sp. nov., ♂. A-C, left and right ocular plate, respectively, in 3 specimens; D, left palp, dorsal view; E, gnathosoma, ventral view; F, detail of epicuticle on anterior dorsal plate between setae ds-1; G, detail of membranous cuticle between plates and seta ds-4; H, detail of epicuticle on anterior epimeral plate. pc, pore canaliculus, P-1 to P-4, palp segments. Scale bars: A(B,C,E), D (F,G,H) = 50 μ m.

pair of glp-1 and pair of ds-1. AD extending beyond level of ds-2 but not to level of ds-3. Pore glp-2 on OC, glp-3 in membranous cuticle between AE and PE (Fig. 7C), glp-4 and glp-5 on PD. OC variable in shape between and within specimens (Fig. 8A-D); pore canaliculus either on OC (right plate in Fig. 8B) or separated from OC in membranous cuticle (Fig. 8A). Posterior to glp-3 a pair of variably shaped plates (Fig. 8A-D). PD with anterior margin rounded (Fig. 7A) or more uneven (Fig. 7E); in posterior half with a series of minute pits laterally. Posterior margin of AE variable; epicuticle similar to AD (Fig. 7B). AE with 3 pairs of setae; PE with 4

setae; no setae in membranous ventral cuticle (Fig. 7C). One pair of outlying pgs in posterior half of GA, 35-42 pgs closely surrounding GO.

Rostrum about as long as gnathosomal base (Fig. 8F). Palp smooth; both setae on P-2 inserted distally (Fig. 8G). P-3 with blunt spine.

Leg segments faintly striated or smooth, in deeper layers punctate, most conspicuously on basifemur I. Chaetotaxy (trochanter - tibia): I 1-2-7 (6,8)-8-15(14) (Fig. 9A), II 1-3(4)-6(7)-6-10(9) (Fig. 9B), III 2-2-5-5-7 (Fig. 9E), IV 1-2-4-6-6 (Fig. 9F). Telofemur I usually with 4 spines (2 heavy and 2 less heavy). On one side of

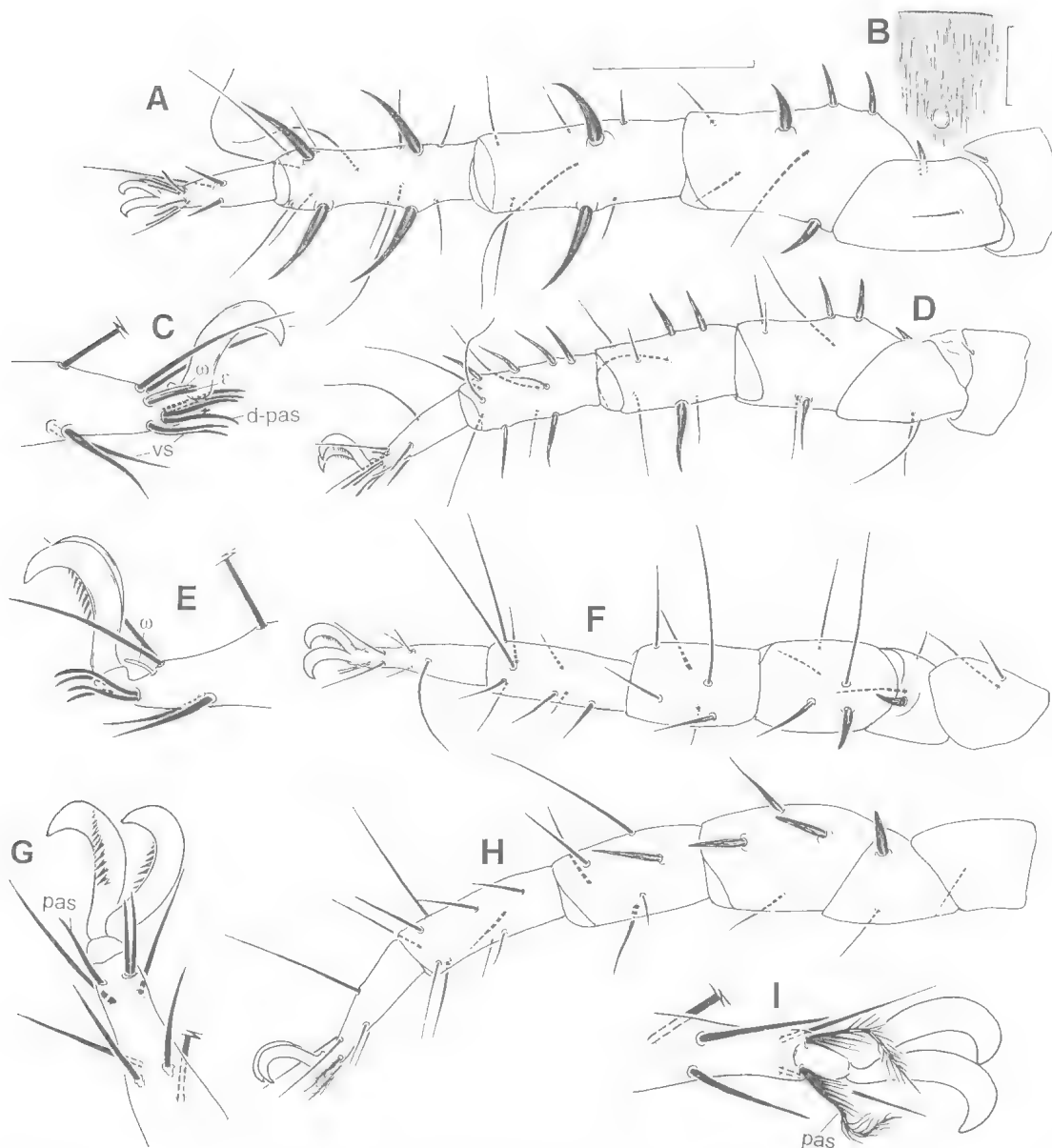


FIG. 5. *Halacarus chilcottensis* sp. nov., ♂; A, right leg I, ventral view; B, detail of cuticle surrounding insertion socket on telofemur I; C, tarsus I, lateral view; D, leg II, ventromedial view; E, tarsus II, medial view; F, left leg III, dorsal view; G, left tarsus III, ventral view; H, leg IV, medial view; I, left tarsus IV, ventral view. d-pas, doubled parambulacral seta; vs, ventral setae on tarsus; ε, famulus; ω, solenidion. Scale bars: A (D,F,H) = 100 μm, B (C,E,G,I) = 20 μm.

one specimen with additional ventral spine (Fig. 9C), and in another specimen one of the 2 less heavy spines lacking on one leg. Telofemur II with single dorsal spine (Fig. 9B), on one leg in one specimen with 2 spines (Fig. 9D). Tibia III with slightly bipectinate medial seta in proximal

half; similar seta medially on genu IV. Telofemur IV with 2 dorsal spines. Tarsus I with 3 dorsal setae, 2 pairs of ventral setae (the distal pair eupathidiform), and pair of doubled pas; solenidion and famulus closely associated and of similar length and thickness (as illustrated for *H.*

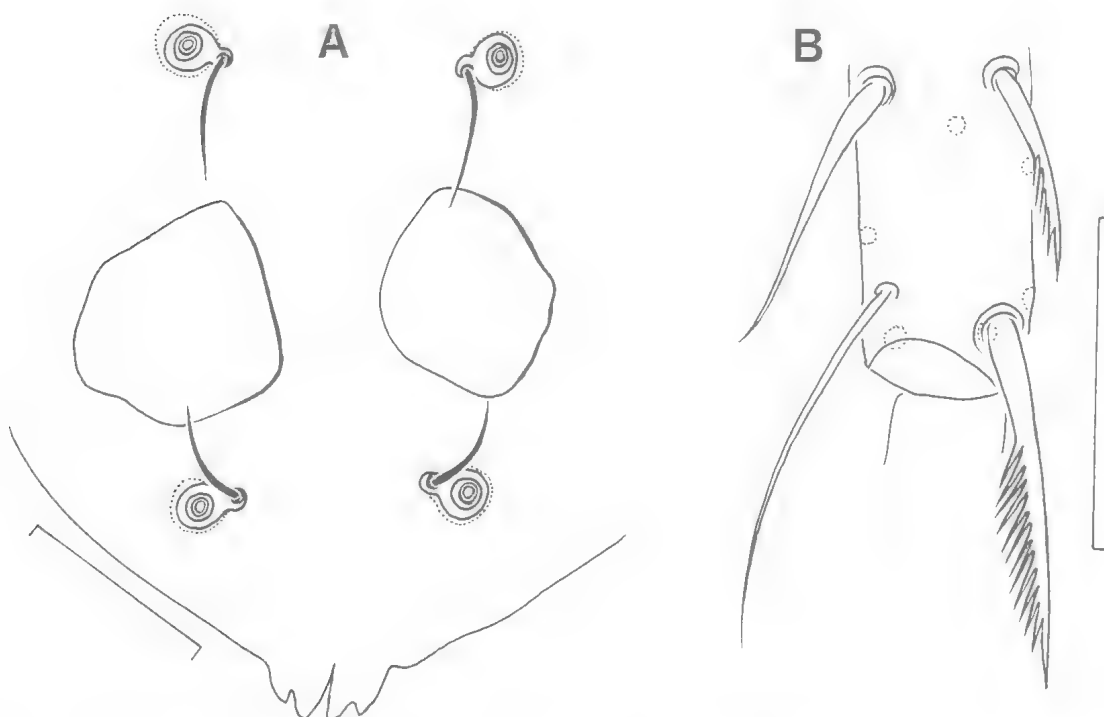


FIG. 6. *Halacarus discophorus* Bartsch, Great Barrier Reef ♂. A, posterior idiosoma, dorsal view; B, right tibia II, ventral view, positions of dorsal setae indicated by their insertion sockets. Scale bars = 50µm.

chilcottensis in Fig. 5C). Tarsus II with 3 dorsal setae, pair of ventral setae and pair of doubled pas of which the ventral branch is more delicate than the dorsal one. Tarsus III with 4 dorsal setae, one doubled pas, one pas singlet, and pair of ventral setae. Tarsus IV with 3 dorsal setae, pair of ventral setae, and pair of plumose pas singlets. Paired claws of legs I and IV smooth, of tarsi II and III with conspicuous pecten. All tarsi with minute empodial claw.

Female. Idiosoma 411µm long. PD more pointed anteriorly than in male; glp-4 and ds-5 on small platelets separated from PD (Fig. 8E). GA with 3 pairs pgs, and 2 pairs sgs (Fig. 7F). Pair of pas on tarsus IV undivided.

REMARKS. *H. heraldensis* belongs to the *membraneus* group. Other species in this group with the glp-3 on the OC are *juliani*, *sabulonis* and *membraneus*. *H. membraneus* differs from *H. heraldensis* in the AD being wide throughout and extending to the level of ds-2, and in having 8 setae on tibia IV and 5 setae on telofemur III.

Bartsch (1981) described only a single pair of ventral setae on tarsus I for *H. membraneus*, in contrast to the 2 pairs in *H. heraldensis*. She also illustrated a ventral spine on telofemur II that

appears shorter than the corresponding spine in *H. heraldensis*. However, both characters are not suitable for separating *H. membraneus* and *H. heraldensis*, as in the holotype of *H. membraneus* 2 pairs of ventral setae occur on tarsus I and the ventral spine on telofemur II is broken off.

***Halacarus juliani* sp. nov.**
(Figs 10, 11)

ETYMOLOGY. In honour of Julian Otto.

MATERIAL. HOLOTYPE, QMS105672, ♀, Great Barrier Reef Marine Park, No Name Reef, ca. 14°39'S 145°40'E, 9 Oct. 1998, medium coarse sand at 6m. **PARATYPES:** Great Barrier Reef Marine Park: QMS105671, 1 ♀, Yonge Reef, ca. 14°36'S 145°38'E, 10 Oct. 1998, coarse sand & rubble at 9m; ANIC, 1 ♀, ♂ Yonge Reef, ca. 14°36'S 145°38'E, G. Diaz-Pulido, medium coarse sand at 7m; ZMH A77/00, 1 ♀, Reef 14-056, 14°19.5'S 144°57.5'E, 21 Oct. 1998, P. Tomkins, medium coarse sand in shallows; QMS 105670, 1 ♀, Reef 13-050, backreef, 13°19'S 143°58.5'E, 29 Aug. 1999, C. Bastidas, K. Fabricius & S. Uthicke, medium coarse sand at 2m.

Female. Idiosoma 416-428µm long (holotype 416µm). AD either developed into a short spine (Fig. 10A) or somewhat more obtuse (Fig. 10B); with ds-1 and glp-1; covered by reticulate epicuticle (Fig. 10F). AD extending beyond level

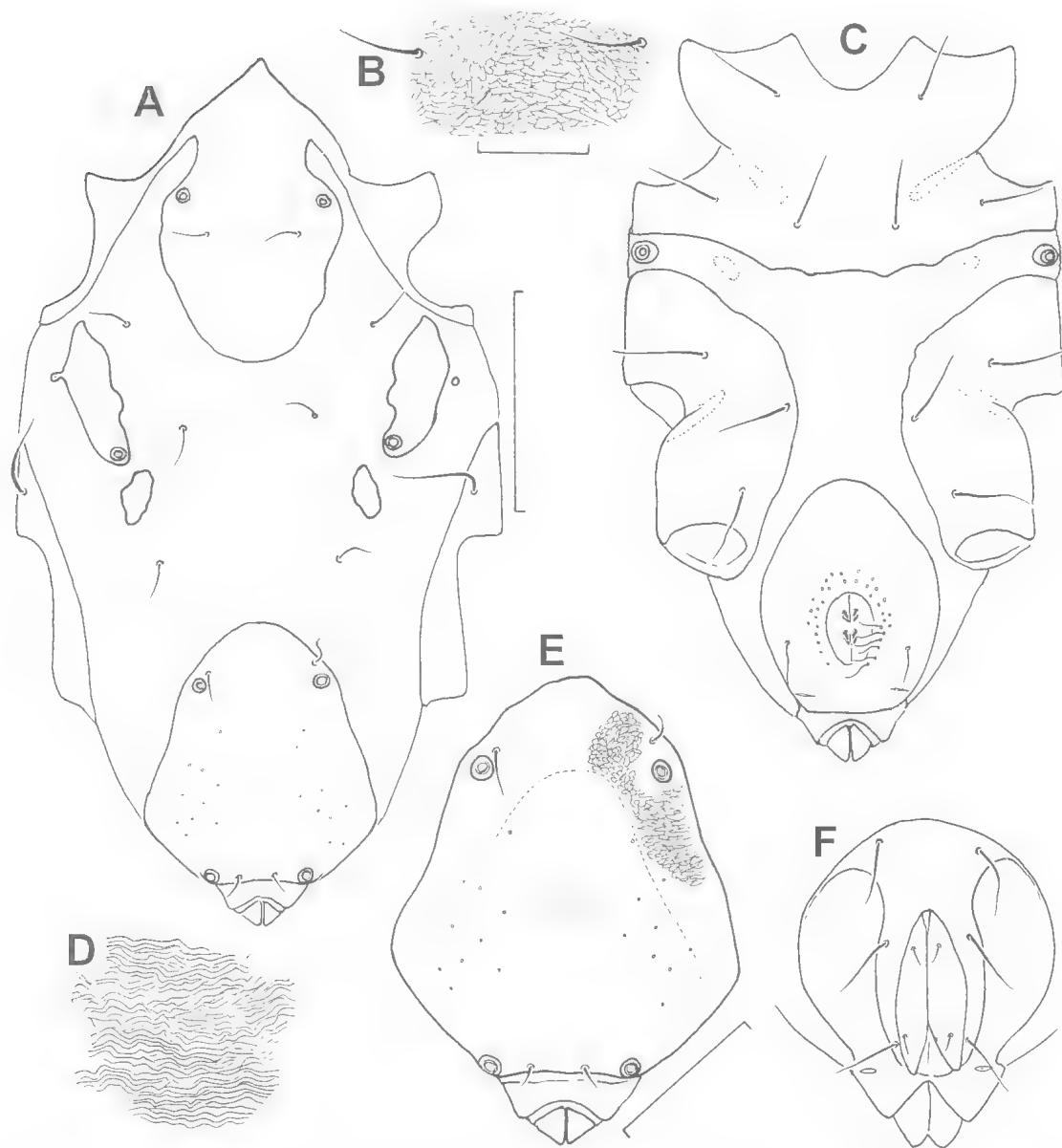


FIG. 7. *Halacarus heraldensis* sp. nov., adult. A, ♂, idiosoma, dorsal view; B, adult; detail of epicuticle between setae ds-1 on anterior dorsal plate; C, ♂, idiosoma, ventral view; D, detail of cuticular striations of membranous dorsal cuticle; E, ♂, posterior dorsal plate; F, ♀, genitoanal plate. Scale bars: A (C) = 100µm; B (D) = 20µm; E(F) = 50µm.

of ds-2 but not to level of ds-3. Setae ds-2, ds-3 and ds-4 in membranous cuticle. OC longer than wide, broadest in anterior half, otherwise variable in shape (Fig. 10A,D); with pore canaliculus anterolaterally and glp-2 posteriorly; postero-medially with muscle scar. Pair of platelets posterior to OC smaller than OC and variable in shape. Pore glp-3 in membranous cuticle

between AE and PE; glp-4 anterolateral to PD on same platelet as ds-5 (Fig. 10E); glp-5 on PD. PD covered with reticulated epicuticle (Fig. 10E); margins, after converging towards anterior, widening into an asymmetrical protrusion (Fig. 10A,E). Posterior margin of AE uneven and variable, epicuticle (Fig. 10G) much more finely reticulate-striate than on AD (Fig. 10F).

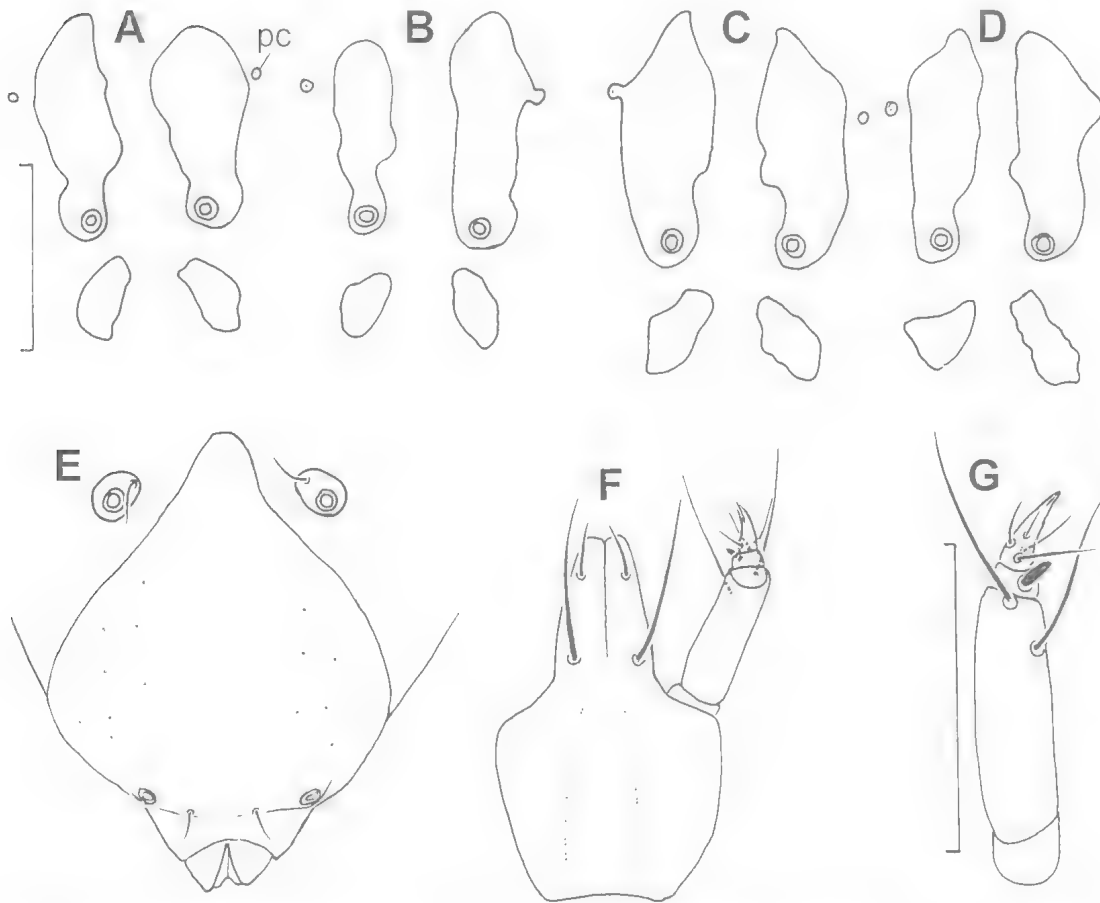


FIG. 8. *Halacarus heraldensis* sp. nov., adult; A-D, ocular plates and posterior platelets in 4 ♂s; E, ♀, posterior dorsal plate; F, ♀, gnathosoma, ventral view; G, ♀, left palp, dorsal view. pc, pore canaliculus. Scale bars: A (B-D, E, F), G = 50 µm.

Rostrum about as long as gnathosomal base. Palp surpassing rostrum (Fig. 10H); smooth; both setae on P-2 inserted distally (Fig. 10I); P-3 with blunt spine.

All leg segments with striated epicuticle. Chaetotaxy (trochanter - tibia): I 1-2-7-8-15 (Fig. 11A), II 1-3-6-6-10 (Fig. 11B), III 2-2-5-5-7 (Fig. 11C), IV 1-2-4-6-6 (Fig. 11D). Telfemur I with 4 spines (2 heavy and 2 less heavy). Telfemora II and III with single dorsal spine. Telfemur IV with 2 dorsal spines. Tarsus I with 3 dorsal setae, 2 pairs of ventral setae (the distal pair eupathidiform), and pair of doubled pas; solenidion and famulus closely associated and of similar length and thickness (as in Fig. 5C). Tarsus II with 3 dorsal setae, pair of ventral setae and pair of doubled pas of which the ventral branch is more delicate than the dorsal one. Tarsus III with 4 dorsal setae, 2 pas singlet or one

doubled pas and one pas singlet, and pair of ventral setae. Tarsus IV with 3 dorsal setae, pair of ventral setae, and pair of setiform (not plumose as in male) pas singlets. Paired claws of legs I, IV smooth, of tarsi II, III with conspicuous pecten. All tarsi with minute empodial claw.

Male. Unknown.

REMARKS. *H. juliani* is a species of the *membraneus* group. Other species in this group which have glp-3 on the OC are *H. membraneus*, *H. sabulonis* and *H. heraldensis*. *H. membraneus* differs from *H. juliani* by having 8 setae on tibia IV and 4 on telfemur III and *H. sabulonis* differs in the epicuticular pattern on the AE (Figs 10G, 15D). *H. heraldensis* can be separated from *H. juliani* by the reticulate epicuticle covering only the anterior and anterolateral, but not the medial part of the PD, as well as by a different

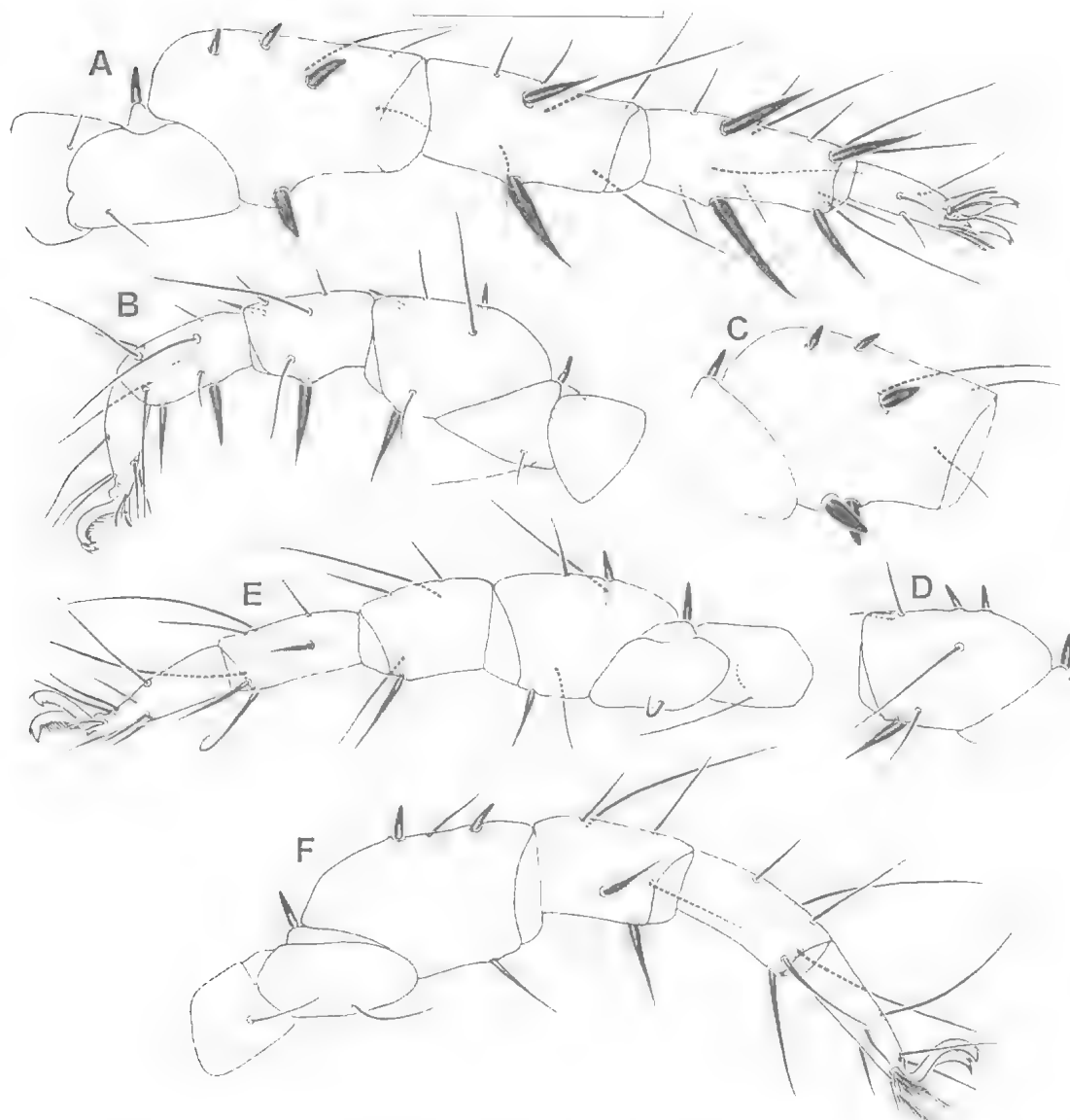


FIG. 9. *Halacarus heraldensis* sp. nov., ♂; A, leg I, ventromedial view; B, leg II, dorsolateral view; C, telofemur I, ventromedial view; D, basifemur II, dorsolateral view; E, leg III, ventromedial view; F, leg IV, ventromedial view. Scale bars: A (B-F) = 100µm.

epicuticular pattern on the AE and a different shape of the anterior part of the PD.

***Halacarus rarus* sp. nov.**
(Figs 12-14)

ETYMOLOGY. *Rarus*, Latin rare; in reference to the single specimen that has been found as yet.

MATERIAL. HOLOTYPE: QMS105638, ♀, Great Barrier Reef Marine Park, 18°25.25'S 146°40.65'E,

Bramble Reef, 10 Apr. 1998, chunks of coral rubble at 3-6m.

DESCRIPTION. *Female*. Idiosoma 512µm long. AD, AE, OC and PD with finely striated epicuticle (Fig. 13A-D), on PE and AE developed into a distinctly fingerprint-like pattern (Fig. 13D). AD anteriorly acuminate (Fig. 12A); pair of large glp-1 half way along plate and distinctly posterior to glp-1 a pair of ds-1 separated by an interval similar to that between

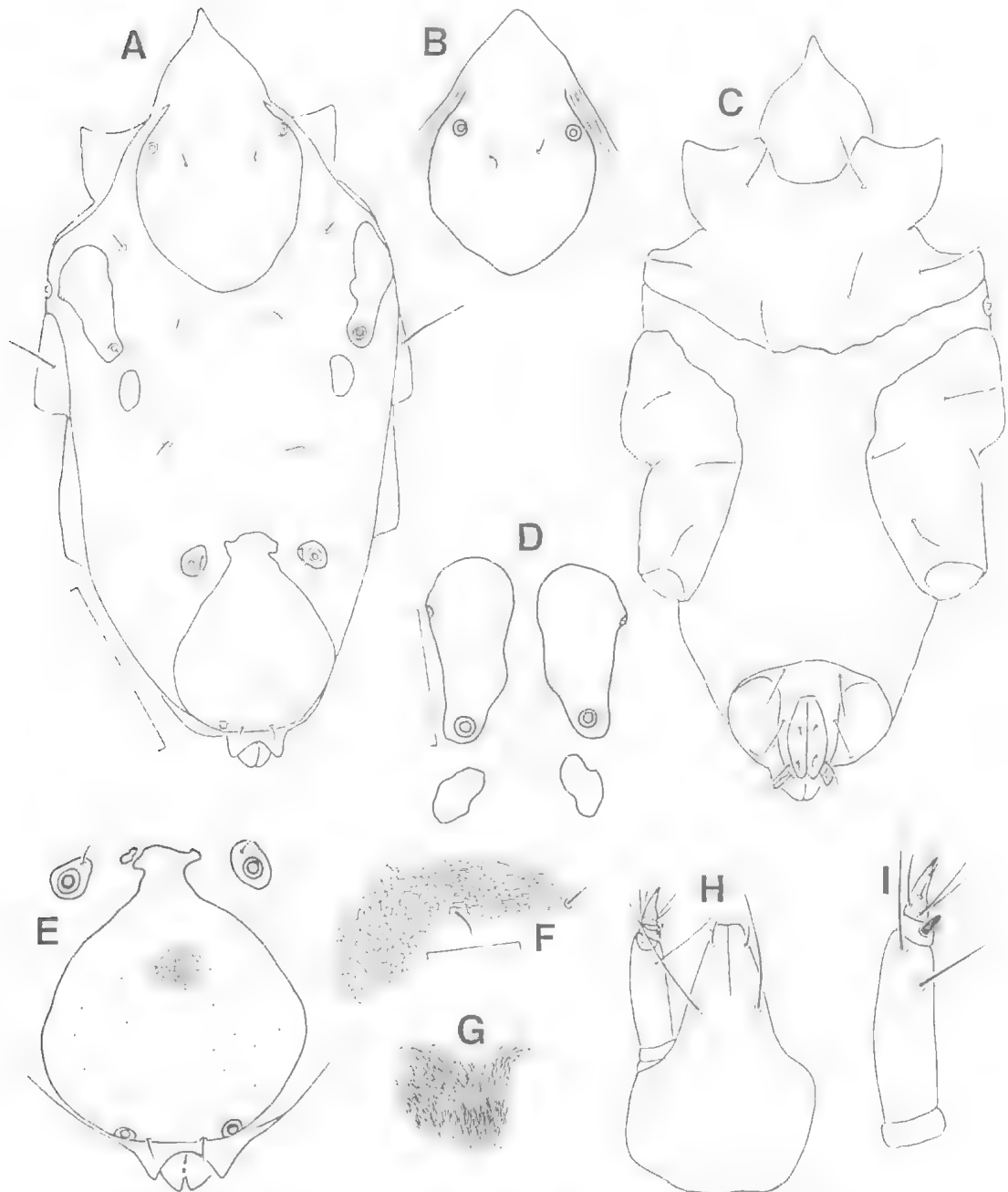


FIG. 10. *Halacarus juliani* sp. nov., ♀. A, idiosoma, dorsal view; B, anterior dorsal plate; C, idiosoma, ventral view; D, left and right ocular plates, respectively, of one specimen; E, posterior dorsal plate; F, detail of epicuticle on anterior dorsal plate near setae ds-1; G, detail of epicuticle on anterior epimeral plate; H, gnathosoma, ventral view; I, palp, dorsal view. Scale bars: A (B,C) = 100 µm; D (E,H) = 50 µm; F(G) = 20 µm.

the outer rims of glp-1 (Fig. 13A). Pore glp-2 on anterior part of PE. OC slightly longer than wide, narrowing posteriorly; anteriorly with inconspicuous cornea, posteriorly with glp-3; part of plate posterior to glp-3 barely visible; pore

canaliculus distinctly anterior to glp-3 near lateral margin. Setae ds-2, ds-3 and ds-4 in membranous cuticle. PD with reticulated pattern underneath striated epicuticle (Fig. 12A); part of PD anterior to glp-4 similar in length to interval

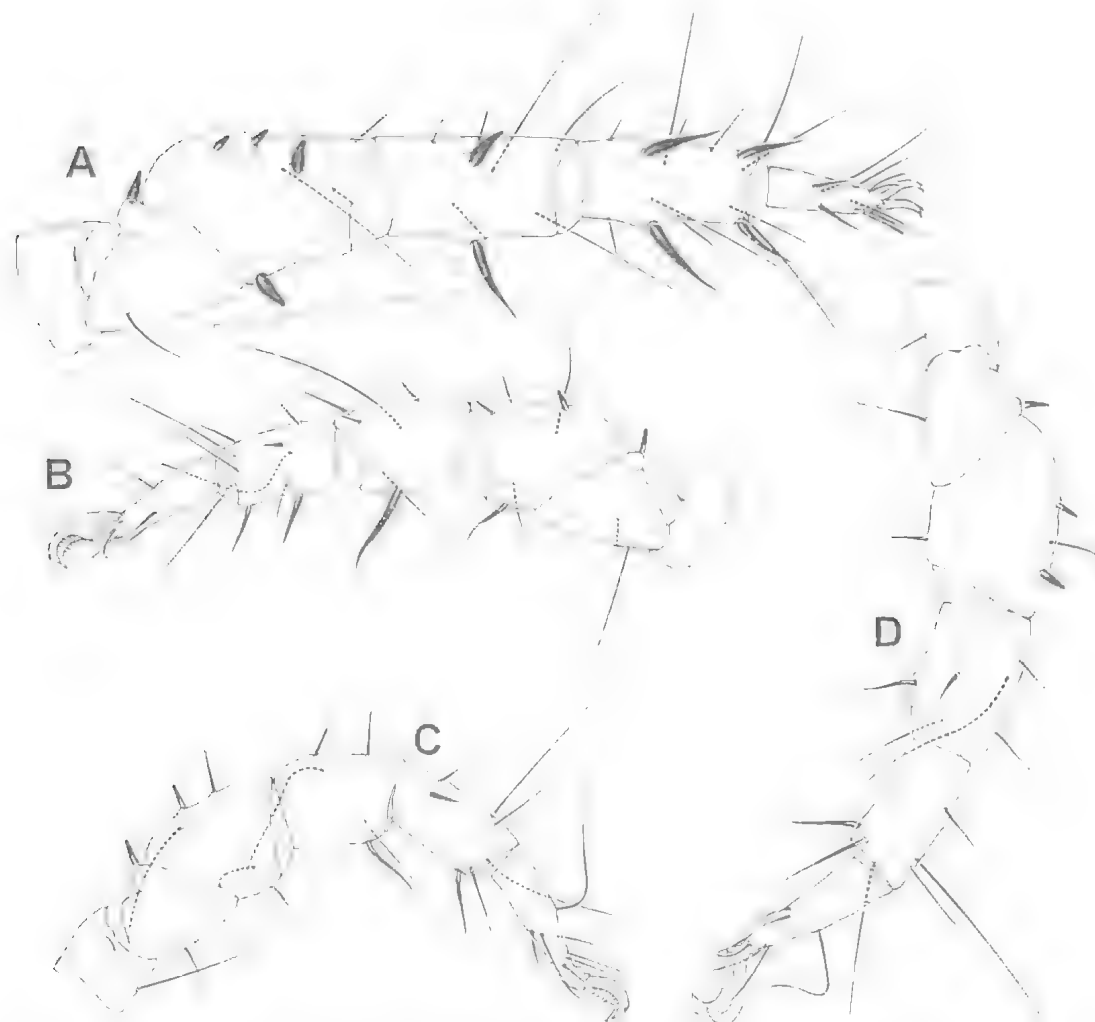


FIG. 11. *Halacarus juliani* sp. nov., ♀. A, leg I, ventromedial view; B, leg II, ventromedial view; C, leg III, ventromedial view; D, leg IV, ventromedial view. Scale bars: A (B,C,D) = 100µm.

between glp-4 and glp-5; ds-5 level with glp-4; ds-6 level with glp-5; glp-4 not protruding laterally. AE with 3 pairs of setae (Fig. 12B) and several conspicuous muscle scars. PE with one dorsal and 3 ventral setae, along anterior margin a conspicuous row of muscle scars. GA with 2 pairs of pgs, and 5 pairs of sgs (Fig. 12B).

Gnathosomal base striated (Fig. 13E). Rostrum slender, slightly longer than gnathosomal base; one pair of maxillary setae proximally, the other distally. Segment P-2 distinctly striated and bulged proximally (Fig. 13F); most proximal seta inserted on protrusion about half way along segment, other much longer seta inserted apically; P-3 with stout spine medially.

Leg chaetotaxy (trochanter - tibia): I 1-2-8-10-12 (Fig. 14A); II 1-4-7-8-11 (Fig. 14B), III 2-2-3-4-7 (Fig. 14C); IV 1-2-3-4-7 (Fig. 14D). Leg I distinctly heavier than other legs; telofemur and genu each with 2 and tibia with 4 ventral spines, the ventromedial one on the telofemur blunt, the others tapering. Thickened or spine-like setae also dorsally on all basifemora and ventrally on genu and tibia II, tibia III and tibia IV; the ventromedial thickened seta on tibia II coarsely bipectinate in distal half. All tarsi with paired claws and small median claw. Paired claws of tarsus I smooth, those of tarsi II-IV with delicate pecten and accessory process.

Male. Unknown.

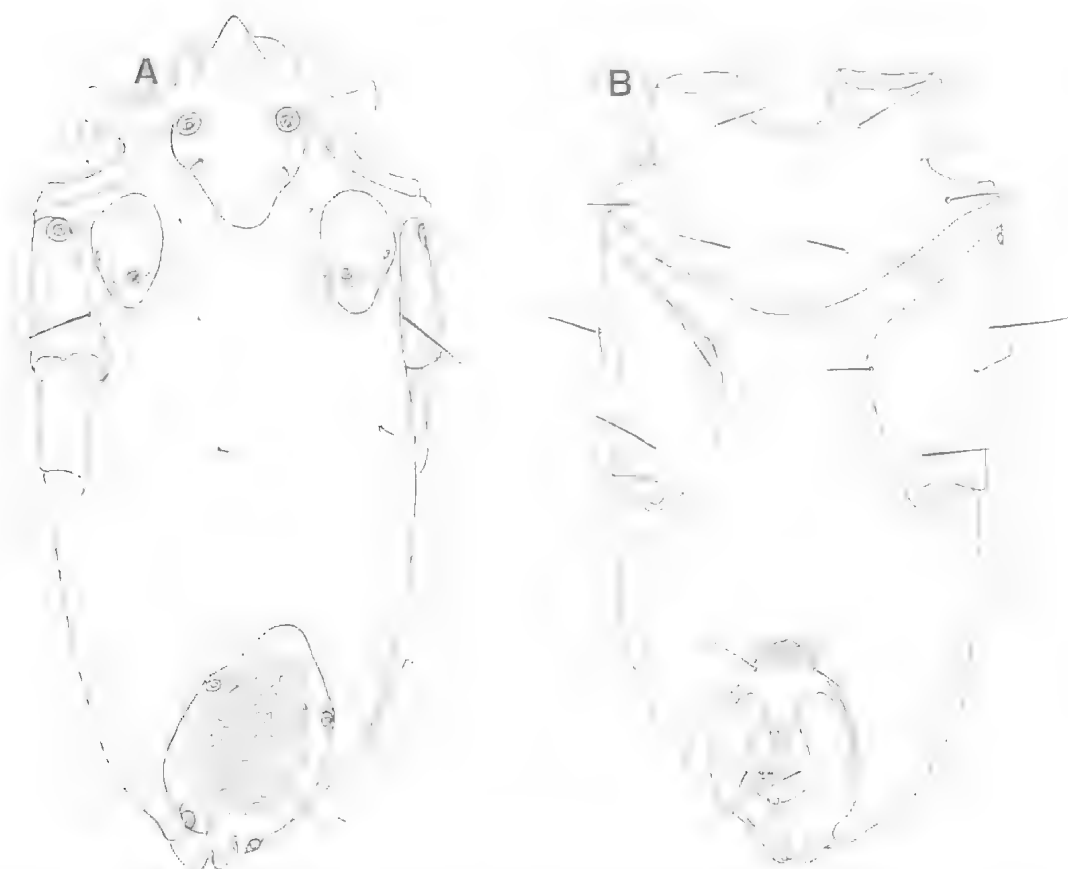


FIG. 12. *Halacarus rarus* sp. nov., ♀; idiosoma: A, dorsal view; B, ventral view. Scale bar: A (B) = 100µm.

REMARKS. *H. rarus* is a member of the *ctenopus* group (Bartsch, 1993b), species of which inhabit warm waters worldwide. The *ctenopus* group is characterised by the combination: AD, OC and PD present; all idiosomal plates, gnathosoma and legs covered with delicately striated epicuticle; 4th pair of gland pores on PD; female GA with 2 pairs of pgs, swollen integument on either side of GO set off from anterior plate; tibia I with 2 pairs of tapering spines; ventromedial spine on tibia II bipectinate. Other species are *ctenopus* Lohmann, 1893, *malaysius* Bartsch, 1993b, *mitrellus* Bartsch, 1993a, *mooreus* Bartsch, 1992, *oblongus* Lohmann, 1893, *subtilis* Viets, 1940, and *turgidus* Viets, 1952 (Newell, 1984). The only other species in this group in which glp-2 is known to be on the anterior part of the PE is *H. mitrellus* from Rottnest Island. *H. mitrellus* differs from *H. rarus* in at least 3 aspects: the female PD extends almost to the level of ds-4; the pore canaliculus on the OC is slightly posterior to

glp-3; the ventral spines on telofemur I are, according to Bartsch's (1993a) illustration, both inserted close to the distal margin.

The SE Australian *H. oblongus* Lohmann, 1893 is similar to *H. rarus*, but differs, according to Lohmann's (1893) illustration, in that pores glp-4 protrude from the PD on either side and setae ds-1 are inserted closer together than in *H. rarus*. I have been unable to locate the type material and hence to verify these characters.

***Halacarus sabulonis* sp. nov.**
(Figs 15, 16)

ETYMOLOGY. *Sabulum*, Latin = coarse sand, gravel; referring to the species' habitat.

MATERIAL. **HOLOTYPE:** QMS105630, ♂, Great Barrier Reef Marine Park, ca. 15°24'S 145°27'E, Boulder Reef, 8 Oct. 1998, A. Thompson, coarse sand at 2m. **PARATYPES:** Great Barrier Reef Marine Park: QMS105627-105629, 105631, 4 ♂, QMS105632-105635, 4 ♀, ZMH A78/00, 1 ♂, 1 ♀, ANIC, 1 ♂, 1 ♀, data as for holotype; QMS105636/105637, 2 ♂, ca.

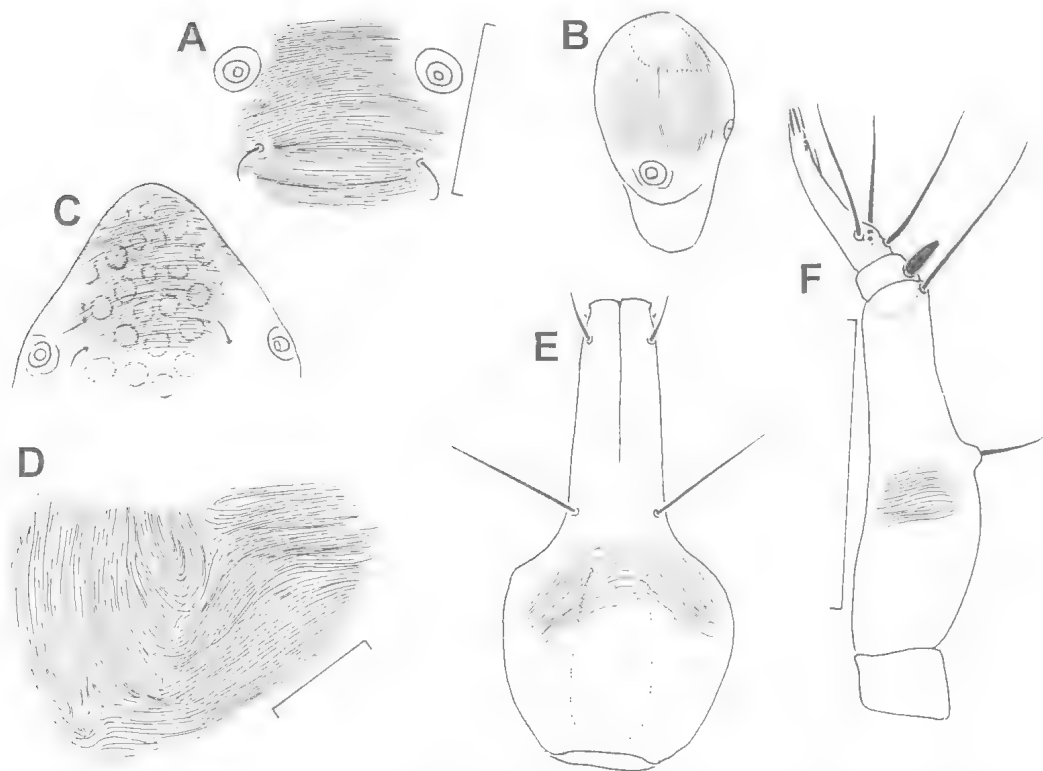


FIG. 13. *Halacarus rarus* sp. nov., ♀. A, detail of cuticle on anterior dorsal plate between glp-1 and ds-1; B, right ocular plate; C, anterior part of posterior dorsal plate; D, detail of cuticle of ventral part of posterior epimeral plate; E, gnathosoma, ventral view; F, right palp, ventromedial view. Scale bars: A (B,C,E), F = 50µm; D = 20µm.

21°09.80'S 151°41.77'E, Reef 21-155, 20 Apr. 1999, coarse sand (mainly *Halimeda* flakes) at 15m.

DESCRIPTION. *Male.* Idiosoma 383-419µm long (holotype 405µm). AD usually drawn out into a short spine (Fig. 15A), in one specimen more obtuse (Fig. 15B) perhaps resulting from a downward deflected and hence invisible tip; posterior margin truncate to convex. AD extending well beyond level of ds-2 but not to level of ds-3; structure of epicuticle (Fig. 15D). Setae ds-2, ds-3 and ds-4 in membranous cuticle. OC variable in shape between and within specimens (Fig. 15A,H); wider anteriorly than posteriorly; anterolaterally with pore canaliculus and posteriorly with glp-3. Posterior to OC with pair of small variable plates. PD with variable anterior margin (Fig. 15A,I,J); anteriorly with glp-4 and ds-5 and posteriorly with glp-5 and closely associated ds-6. Posterior margin of AE variable, ranging from gently rounded to jagged; reticulation of epicuticle (Fig. 15E), only slightly finer than on AD (Fig. 15D). Three pairs of setae on AE, 4 setae on PE, but no setae in membranous

ventral cuticle. GA with a pair of outlying pgs in posterior half, 28-39 pgs closely surrounding GO; sgs not clear.

Rostrum about as long as gnathosomal base. Palp surpassing rostrum (Fig. 15F); smooth; both setae on P-2 inserted distally (Fig. 15G). P-3 with blunt spine.

Only basifemora and telofemora dorsally faintly striate, surface of other segments smooth, in deeper cuticular layers with fine canaliculi. Leg chaetotaxy (trochanter - tibia): I 1-2-7-8-15 (Fig. 16A), II 1-3-6-6-10 (Fig. 16B), III 2-2-5-5-8 (Fig. 16C), IV 1-2-4-6-6 (Fig. 16D). Telofemur I with 4 spines (2 heavy and 2 less heavy). Telofemora II and III with single dorsal spine. Telofemur IV with 2 dorsal spines. Tarsus I with 3 dorsal setae, 2 pairs of ventral setae (distal pair eupathidiform), and pair of doubled pas; solenidion and famulus closely associated and of similar length and thickness (Fig. 5C). Tarsus II with 3 dorsal setae, pair of ventral setae and pair of doubled pas of which the ventral branch is more delicate than the dorsal one. Tarsus III with

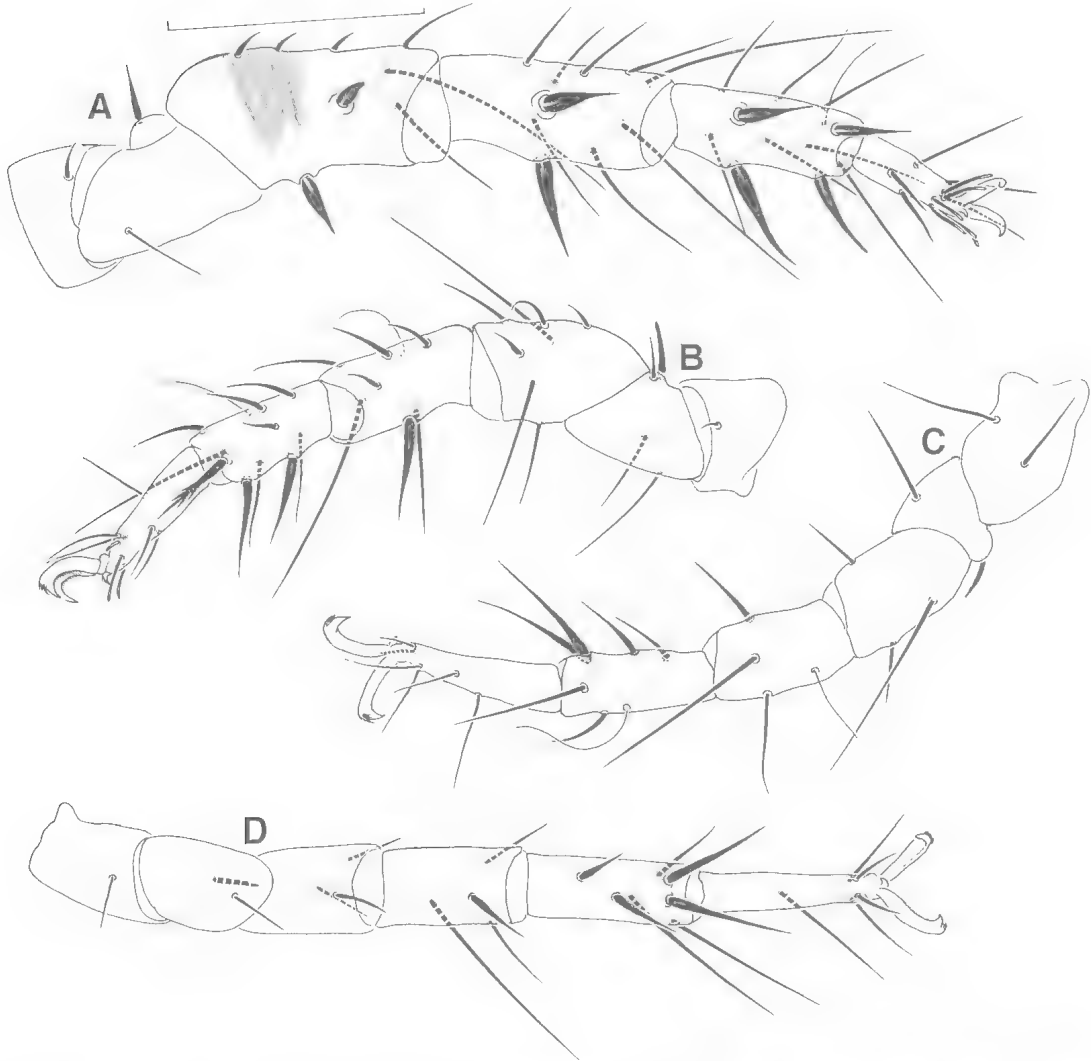


FIG. 14. *Halacarus rarus* sp. nov., ♀. A, leg I, ventromedial view; B, leg II, ventromedial view; C, leg III, dorsolateral view; D, right leg IV, ventral view. Scale bar: A(B-D) = 100µm.

4 dorsal setae, a doubled pas, a pas singlet, and pair of ventral setae. Tarsus IV with 3 dorsal setae, pair of ventral setae, and pair of plumose pas singlets. Paired claws of legs I and IV smooth, those of tarsi II and III with conspicuous pecten. All tarsi with minute empodial claw.

Female. Idiosoma 379-448µm long. Pair of glp-4 separated from PD (Fig. 15K). Pair of ds-5 usually on same platelet as glp-4 (Fig. 15K), in one specimen ds-5 separated from glp-4 on one side. GA with 3 pairs pgs and 2 pairs sgs. Pair of pas on tarsus IV setiform, not plumose as in male.

REMARKS. *Halacarus sabulonis* sp. nov. belongs to the *membraneus* group. Other species

in the group with glp-3 on the OC are *juliani*, *heraldensis* and *membraneus*. *H. sabulonis* differs from them by having eight instead of 7 setae on tibia III and by the reticulated epicuticle of the AE consisting of cells that are approximately as long as they are wide and hence not as slender as in the other 3 species.

***Halacarus striolus* sp. nov.**
(Figs 17, 18)

ETYMOLOGY. *Stria*, Latin = line; referring to the striated epicuticle on the legs.

MATERIAL: HOLOTYPE: QMS105624, ♂, Great Barrier Reef Marine Park, Bylund Cay, ca. 21°47'S

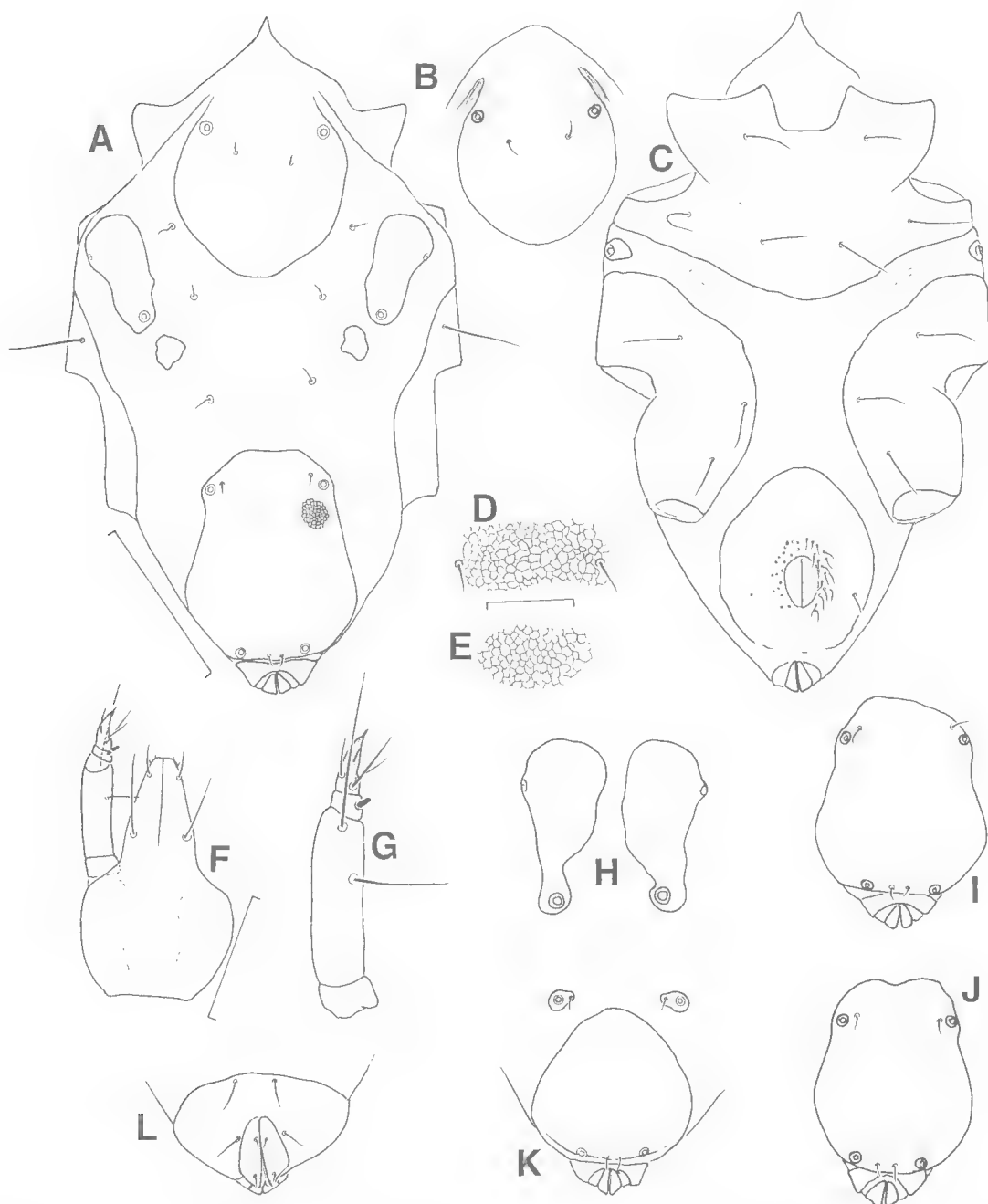


FIG. 15. *Halacarus sabulonis* sp. nov., adult. A, ♂, idiosoma, dorsal view; B, ♂, anterior dorsal plate; C, ♂, idiosoma, ventral view; D, detail of epicuticle on anterior dorsal plate between setae ds-1; E, detail of epicuticle of anterior epimeral plate; F, ♂, gnathosoma, ventral view; G, ♂, palp, dorsal view; H, left and right ocular plates, respectively, of one ♂; I, J, ♂, posterior dorsal plate of two specimens; K, ♀, posterior dorsal plate; L, ♀, genitoanal plate. Scale bars: A (B,C, I-L) = 100µm; D (E,G) = 20µm; F (H) = 50µm.

152°24'E, 17 Apr. 1998, coarse sand just above low tide mark, sediment depth 10-20cm. PARATYPES: Great Barrier Reef Marine Park: QMS105625, 1 ♀, data as for

holotype; QMS195626, 1 ♂, Reef 21-149, 21°06'S 151°43'E, reef flat, 22 Apr. 1999, coarse sand at 0.5m; ZMH A79/00, 1 ♂, East Cay, 21°29'S 152°33'E, 18 Apr.

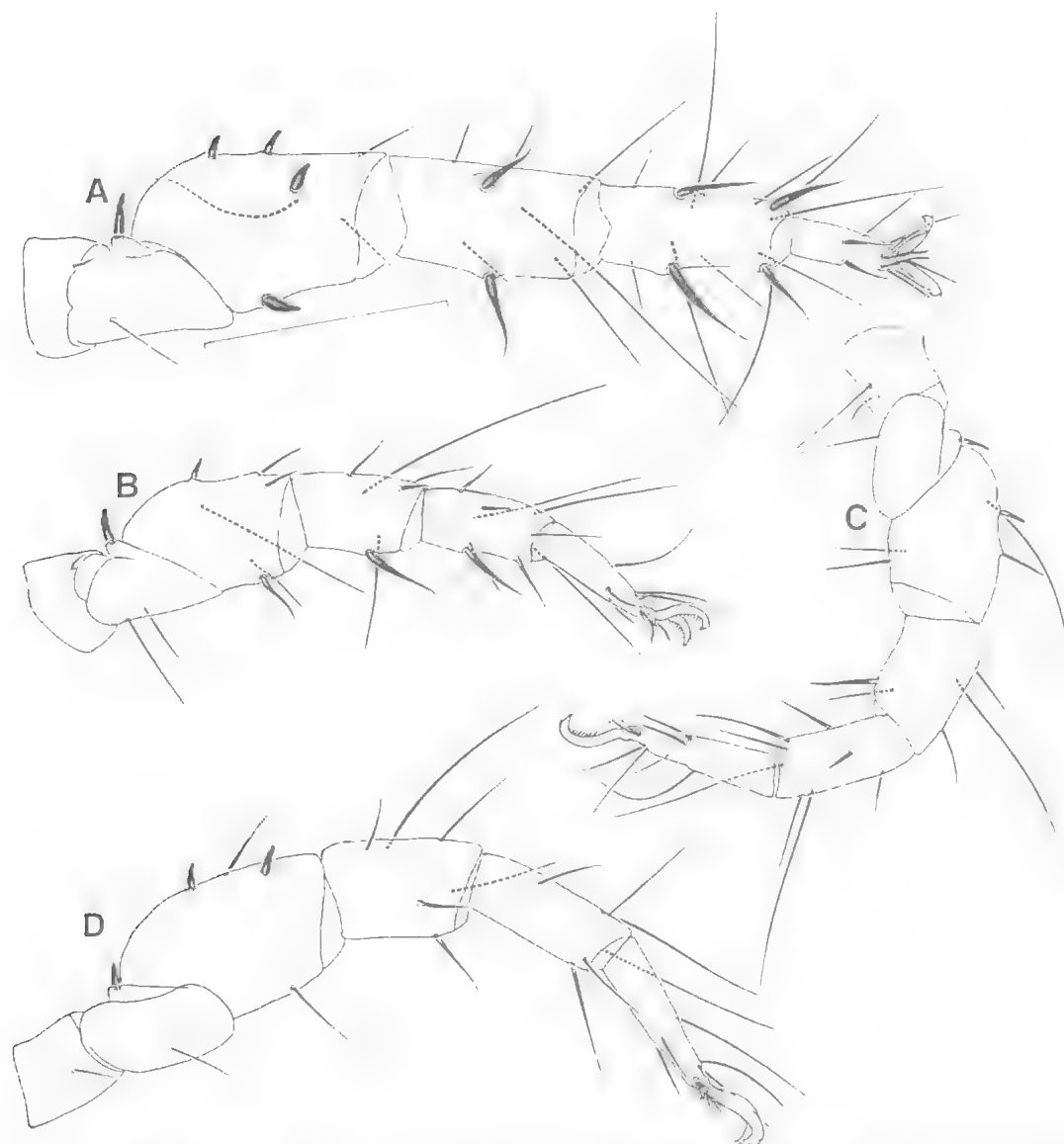


FIG. 16. *Halacarus sabulonis* sp. nov., ♂. A, leg I, ventromedial view; B, leg II, ventromedial view; C, leg III, ventromedial view; D, leg IV, ventromedial view. Scale bar: A (B-D) = 100µm.

1999, reef flat off front, coarse sand; ANIC, 1 ♂, ZMH, 1 ♀, Chinaman Reef, ca. 22°00'S 152°40'E, reef flat, 10 Dec. 1998, G. Coleman, coarse sand (mainly *Halimeda* flakes) at 3m.

DESCRIPTION. *Male.* Idiosoma 372-403µm long (holotype 394µm). AD, OC, PD and AE covered by reticulated epicuticle (Fig. 17A). AD developed into a stout spine, usually shaped as in Fig. 17A, in one specimen as in Fig. 17B. Setae ds-2, ds-3 and ds-4 in membranous cuticle. OC widest in anterior half, otherwise of variable

shape; anterolaterally with pore canaliculus. Pair of glp-3 separated from OC, except for one specimen where on one side OC and glp-4 are narrowly fused. Anterior margin of PD variable (Fig. 17G, H). Epicuticle on AE (Fig. 17D) finer than on AD (Fig. 17E). One pair of outlying pgs in posterior half of GA, 32-43 pgs closely surrounding GO; sgs not clearly seen.

Rostrum about as long as gnathosomal base. Both setae on P-2 inserted distally (Fig. 17J); P-3 with blunt spine.

All leg segments with striated epicuticle (shown for tibia I in Fig. 18E); underneath epicuticle punctate, most distinctly on basifemora and telofemora. Leg chaetotaxy (trochanter - tibia): I 1-2-7-8-15 (14) (Fig. 18A), II 1-3 -6-6-10 (9) (Fig. 18B), III 2-2-5-5-8 (Fig. 18C), IV 1-2-4-6-6 (Fig. 18D). Telofemur I with 4 spines (2 heavy and 2 less heavy). Telofemora II and III with single dorsal spine. Telofemur IV with 2 dorsal spines. Tarsus I with 3 dorsal setae, 2 pairs of ventral setae (the distal pair eupathidiform), and pair of doubled pas; solenidion and famulus closely associated and of similar length and thickness (Fig. 5C). Tarsus II with 3 dorsal setae, pair of ventral setae and pair of doubled pas of which the ventral branch is more delicate than the dorsal one. Tarsus III with 4 dorsal setae, a doubled pas and a pas singlet or 2 pas singlets, and pair of ventral setae. Tarsus IV with 3 dorsal setae, pair of ventral setae, and pair of plumose pas singlets. Paired claws of legs I and IV smooth, those of tarsi II and III with conspicuous pecten. All tarsi with minute empodial claw.

Female. Idiosoma 342-399 μm long. Pair of glp-4 separated from PD (Fig. 17A, F). Seta ds-5 either on the same platelet as glp-4 (Fig. 17A) or separated from it in membranous cuticle (Fig. 17F). GA with 3 pairs of pgs and 2 pairs of sgs.

Pas on tarsus IV setiform, not plumose as in σ .

REMARKS. *H. striolus* is a member of the *membraneus* group. It appears to be most similar to *H. sabulonis* but can be distinguished by the separation of the OC and glp-3 and by having striated epicuticle on all genua and tibiae.

The only other species in the *membraneus* group that has glp-3 separated from the OC is *H. chilcottensis*. *H. striolus* differs from it by lacking spines dorsally on tibia I, a different number of setae on telofemur, genu, and tibia II, basifemur, genu, and tibia III and tibia IV, and in the different structure of the epicuticle on the AE (Figs 4H, 15I).

***Halacarus tritoni* sp. nov.**

(Figs 19A-D, 20)

ETYMOLOGY. *Triton*, Latin, Greek, a sea-god.

MATERIAL. HOLOTYPE: QMS105639, ♀, GBR Marine Park, 19°20.12'S 149°02.85'E, Elizabeth Reef, 25 Dec. 1997, epiflora on staghorn coral at 10m.

DESCRIPTION. *Female*. Idiosoma 452 μm long. Dorsal setae in relation to the idiosoma longer than in preceding species (Fig. 19A). PD absent.

AD poorly defined, developed anteriorly into distinct spine; covered by finely reticulate epicuticle similar to that shown for AE in Fig. 19C; ds-1 slightly anterior to glp-1; posterior part of AD with conspicuous muscle scars. OC absent but conspicuous oval cornea anterolateral to pore canaliculus. Seta ds-3 at same level as glp-3. Seta ds-5 widely separated from glp-4. Margins of ventral plates poorly defined; posterior margin of AE lined by a row of muscle scars. One pair of ventral setae in membranous cuticle. GO with 2 pairs of pgs, and 5 pairs sgs. Four pairs of eugenital setae protruding through GO (not illustrated).

Rostrum longer than gnathosomal base and both pairs of maxillary setae separated by an interval greater than that between proximal maxillary seta and proximal margin of gnathosomal base (Fig. 19D). Segment P-2 with both setae in distal half. Spine on P-3 with distinctly convex margins.

Leg chaetotaxy: (trochanter - tibia): I 1-2-10-10-13 (Fig. 20A), II 1-3-8-10-12 (Fig. 20B), III 2-2-7-9-11 (Fig. 20C), IV 1/2-2-5-7-10 (Fig. 20D); all basifemora with blunt dorsal spine. Leg I with 2 tapering spines ventrally on each of telofemur and genu, and 4 similar spines ventrally on tibia. Thickened setae also on genu and tibia II and to lesser extent on genua and tibiae III, IV. Tibia II with 2 bipectinate ventromedial setae, the distal one longer than the proximal one, and with 7-8 spines on either side. Tarsus I with 3 dorsal setae, 2 pairs of ventral setae and pair of doubled pas. Tarsus II with 4 dorsal setae, 3 pairs of ventral setae (the distal pair eupathidia) and pair of doubled pas. Tarsus III with 4 dorsal setae, 2 pairs of ventral setae, a doubled pas in which one branch is shorter than the other, and a pas singlet. Tarsus IV with 3 dorsal setae and pair of pas singlets, one leg with 2 pairs of ventral setae, the other with 3 ventral setae. Paired claws of all legs with accessory process consisting of 4-5 spines (Fig. 20E); no pecten along shaft.

REMARKS. *H. tritoni* belongs to the *actenos* group (Bartsch, 1993a) and is most similar to *H. socius* Bartsch, 1992, from the Society Islands. Both species share a similarly shaped AD with ds-1 slightly anterior to glp-1, 2 bipectinate setae on tibia II and the lack of such a seta on genu II. *H. socius* differs from *H. tritoni* by having 6 setae on telofemur III, 4 setae on telofemur IV, 5 setae on genu IV, a row of 3-4 spines on either side on the distal bipectinate seta on tibia II, straight instead

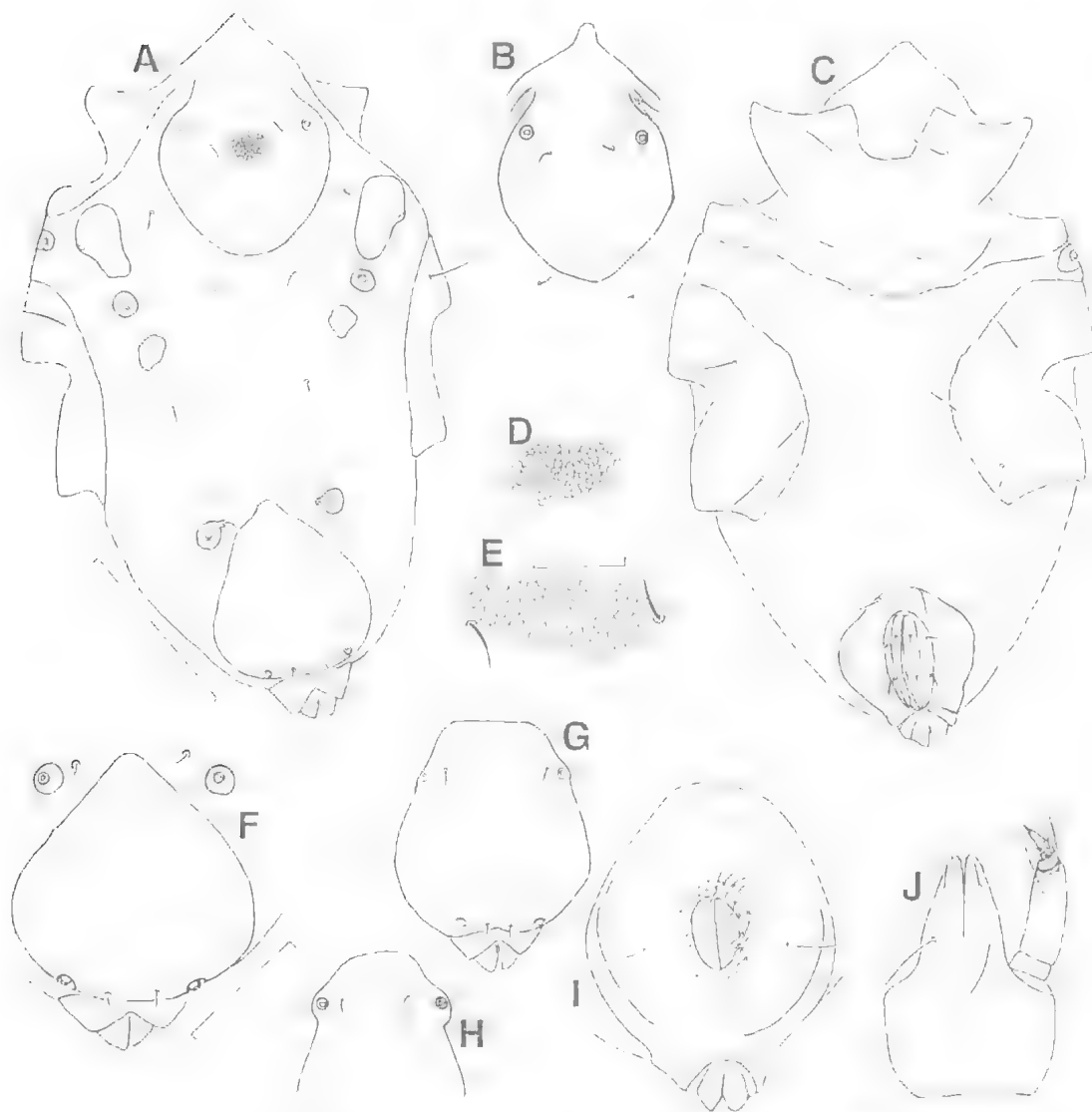


FIG. 17. *Halacarus striolus* sp. nov., adult. A, ♀, idiosoma, dorsal view; B, anterior dorsal plate; C, ♀, idiosoma, ventral view; D, detail of epicuticle of anterior epimeral plate; E, detail of epicuticle on anterior dorsal plate between ds-1; F, X, posterior dorsal plate; G, H, posterior dorsal plates of two ♂♂ (anterior part only in Fig. 17G); I, ♂, genitoanal plate; J, ♂, gnathosoma, ventral view. Scale bars: A (B,C,G,H) = 100 µm; E (D) = 20 µm; F (I,J) = 50 µm.

of convex margins of the spine on palp segment P-3, and by having setae ds-3 inserted distinctly posterior to pores glp-3.

For *H. socius* Bartsch (1992) reported 9 setae on telofemur I and illustrated both bipectinate setae on tibia II as of equal length and thickness, which would distinguish it further from *H. tritoni*. However, I examined the holotype of *H. socius* and found 10 setae (or alveoli) on each telofemur I and the distal bipectinate seta on tibia

II to be distinctly longer and heavier than the proximal one, similar to *H. tritoni* (Fig. 17B).

Halacarus tritoni is similar to *H. magniporus* Krantz, 1973 (see also MacQuitty, 1984) in the shape of the spine on P-2, but differs by having setae ds-5 clearly separated from glp-4 and lacking a bipectinate seta on genu II.

Other species of the *actenos* group similar to *H. tritoni* are *actenos* Trouessart, 1889 (Bartsch, 1979), *higginsii* Newell, 1984, and *zealandicus*

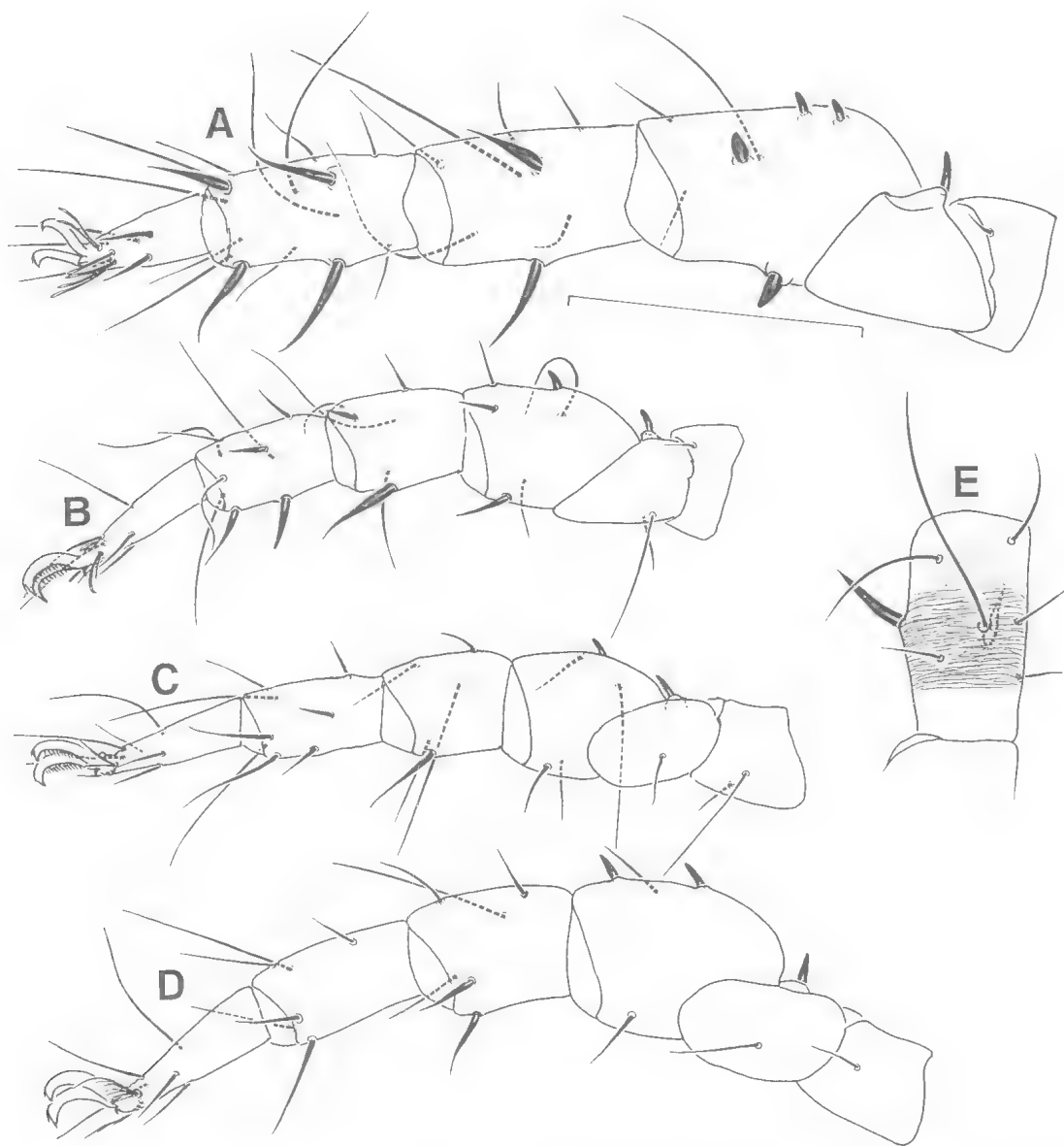


FIG. 18. *Halacarus striolus* sp. nov., adult. A, ♀, leg I, ventromedial view; B, ♂, leg II, ventromedial view; C, ♂, leg III, ventromedial view; D, ♂, leg IV, ventromedial view; E, ♂, tibia I, dorsolateral view. Scale bars: A (B-E) = 100 μm.

Newell, 1984. *H. tritoni* differs from all of them by the spine on P-2 having distinctly concave margins. It differs from *H. higginsii* in the number of setae on telofemora I-IV (11-9-6-4 in *H. higginsii* respectively), from *H. zealandicus* by a shorter frontal spine, and from *H. actenos* in having five instead of 4 setae on telofemur IV (Bartsch, 1979), and lacking a bipectinate seta on genu II.

H. tritoni has 4 dorsal setae on tarsus III, which is unusual for species of the actenos group and *Halacarus* in general. It is unknown whether this represents an anomaly of the holotype or a distinguishing character of *H. tritoni*.

I have examined a ♀ (QMS105669, GBR Marine Park, 18°42.11'S 146°31.51'E, Fantome Island, 15 Apr. 1998, chunks of coral rubble at 2m) (Fig. 19E) which agrees in most aspects with

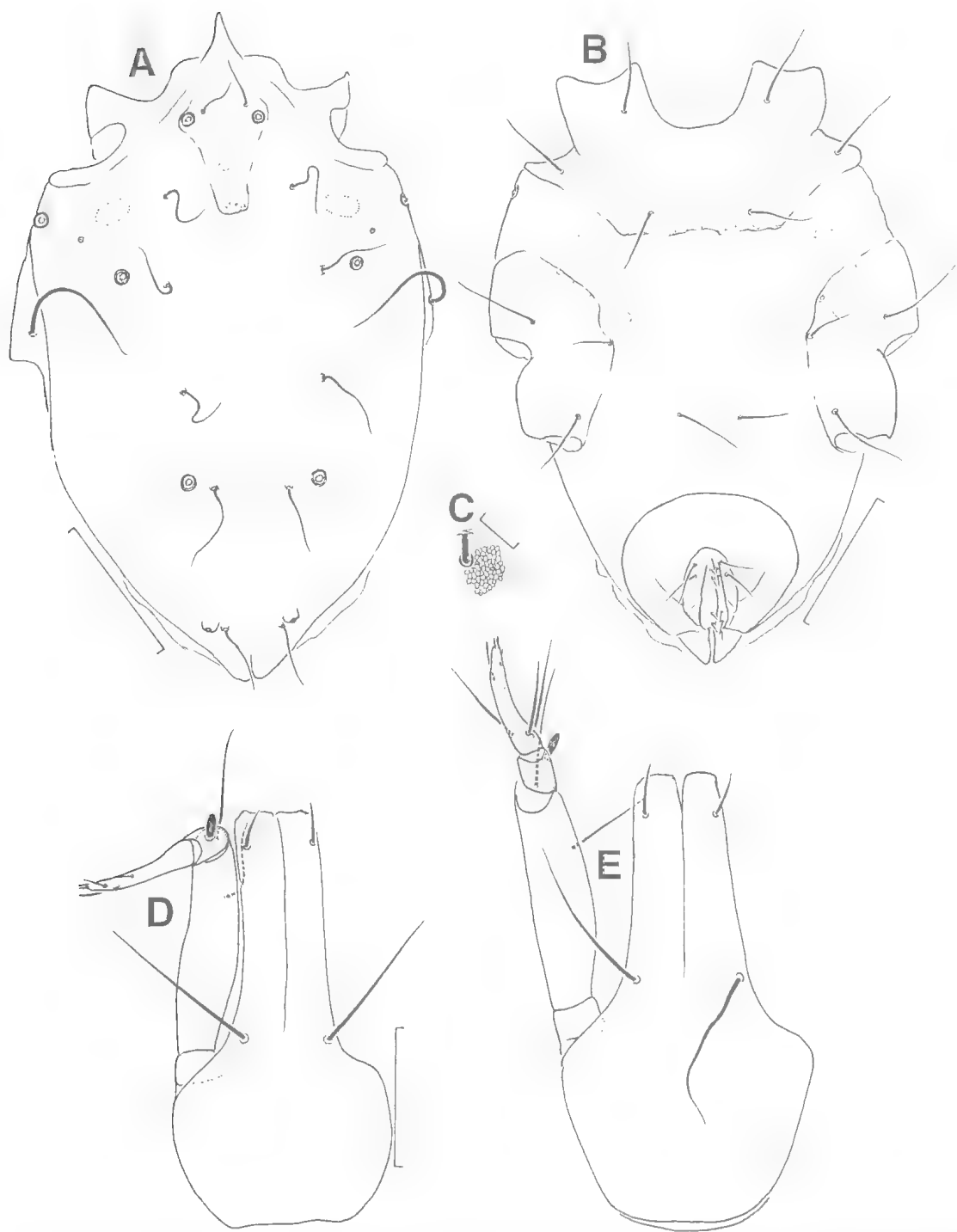


FIG. 19. *Halacarus tritoni* sp. nov., ♀. A, idiosoma, dorsal view; B, idiosoma, ventral view; C, detail of epicuticle on anterior epimeral plate near anterior pair of setae; D, ventral gnathosoma; E, *Halacarus* sp. ♀, (QMS105669), ventral gnathosoma. Scale bars: A, B = 100µm; C = 10µm; D (E) = 50µm.



FIG. 20. *Halacarus tritoni* sp. nov., ♀. A, leg I, ventromedial view; B, leg II, ventromedial view; C, leg III, ventrolateral view; D, leg IV, lateral view; E, apical part of paired claw II. Scale bars: A (B,C,D) = 100µm; E = 20µm.

the holotype of *H. tritoni*, but differs in several characters: The specimen is 603µm long, has 3 dorsal and 5 ventral setae on tarsus II, and has, in relation to its gnathosoma, a shorter rostrum with the 2 pairs of maxillary setae inserted closer together (Fig. 16E). It is unknown whether this specimen belongs to *H. tritoni* or to a further species in the *actenus* group.

KEY TO AUSTRALIAN SPECIES OF *HALACARELLUS*

1. Dorsal plates with reticulate or foveate ornamentation; OC ca. 2-2.5 × longer than wide 2
Dorsal plates smooth apart from series of minute pits; OC more than 3 times longer than wide (Fig. 1A)
. *H. katewilsonae* sp. nov.
2. Telofemur IV shorter than 1.3 × the length of genu IV *H. rotmestensis* Bartsch, 1990
Telofemur IV longer than 1.5 × the length of genu IV *H. lubrius* Bartsch, 1985

KEY TO AUSTRALIAN SPECIES OF *HALACARUS*

Halacarus oblongus Lohmann is excluded as it is insufficiently described and I have been unable to locate the type material; *Halacarus* sp. A and sp. B (Bartsch, 1993a) are excluded as they are only known from juveniles.

1. Idiosoma without PD (Fig. 19A); if platelets are present in the posterior half of dorsum, then only in male, and only as a pair between ds-5 and ds-6 (Fig. 6A) 2
Idiosoma with PD (Fig. 3A, 7A, 12A) 6
2. AD anteriorly obtuse; tibia II without pectinate setae *H. celanus* Bartsch, 1993a
AD anteriorly developed into conspicuous spine (Fig. 19A); at least one seta on tibia II pectinate (Fig. 20B) 3
3. Pore glp-4 and seta ds-5 closely associated on the same sclerite (Fig. 6A); spinose seta on tibia I pectinate only on one side (Fig. 6B); male with pair of platelets between setae ds-5 and ds-6 (Fig. 6A) *H. discophorus* Bartsch, 1993a
Pore glp-4 and seta ds-5 clearly separated (Fig. 19A) and not on the same sclerite; spinose seta on tibia I pectinate on two sides (Fig. 20B); male without pair of platelets between ds-5 and ds-6 4
4. Setae ds-1 inserted slightly anterior to pores glp-1 (Fig. 19A); genu II without pectinate seta (Fig. 20B); tarsi III and IV with at least 3 ventral setae, excluding pas (Fig. 20C,D) *H. tritoni* sp. nov.
Setae ds-1 inserted distinctly posterior to glp-1; genu II with pectinate seta; tarsi III and IV with one ventral seta (excluding pas) 5
5. Pores glp-1 on AD; both setae on P-2 separated by an interval greater than the width of P-2, telofemur III with 6-7 setae *H. fuscatus* Bartsch, 1993a
Pores glp-1 lateral to PD in membranous cuticle; both setae on P-2 separated by an interval less than the width

- of P-2; telofemur III with five setae
 *H. flavellus* Bartsch, 1993a
6. OC present, posterior to it a platelet (Figs 3A, 7A);
 telofemur I with 4 spines (Fig. 5A, 9A) 7
 OC absent or present; if present then posterior to it
 without platelet; telofemur I with two spines 11
7. Pores glp-3 on OC (Fig. 7A, 8A-D). 8
 Pores glp-3 separated from OC (Fig. 3A, 17A) 10
8. Tibia III with eight setae; cells' forming the epicuticular
 pattern on AE of similar length and width (Fig. 17D)
 *H. sabulonis* sp. nov.
 Tibia III with seven setae; cells' that form the epicuticular
 pattern on AE slender (as for AD in Fig. 7B; Fig. 10G) 9
9. PD covered entirely by reticulate epicuticle; epicuticular
 structure on AE (Fig. 10G) with pattern conspicuously
 finer than on AD; lateral margins of female AD towards
 anterior at first converging but then expanding into
 unsymmetrical protrusion (Fig. 10A,E); known only
 from the Great Barrier Reef *H. juliani* sp. nov.
 PD only anteriorly and laterally with reticulate epicuticle
 (Fig. 7E); epicuticular structure on AE similar to that on
 AD (7B); female PD continuously narrowing anteriorly
 (Fig. 8E), known only from the Queensland Plateau
 *H. heraldensis* sp. nov.
10. Tibia I dorsally with 3-5 spines or thickened setae (Fig.
 5D); eight setae on genu II, ten setae on tibia IV
 *H. chilcottensis* sp. nov.
 Tibia I dorsally without spines (Fig. 14A); six setae on
 genu II; six setae on tibia IV *H. striolus* sp. nov.
11. Rostrum shorter than gnathosomal base; OC absent 12
 Rostrum longer than gnathosomal base; OC well
 developed 14
12. Seta ds-5 and pore glp-4 inserted together on one sclerite
 13
 Seta ds-5 near but not on same sclerite as pore glp-4
 *H. arenarius* Bartsch, 1993a
13. Seta ds-1 anterior to glp-1; AD slender, not markedly
 expanded at level of glp-1 *H. parvulus* Bartsch, 1993a
 Seta ds-1 posterior to glp-1; AD expanded at level of
 glp-1 *H. helenae* Bartsch, 1993a
14. Dorsal plates and legs conspicuously striated (Fig.
 13A-C, 14A); setae in dorsal membranous cuticle
 shorter than OC (Fig. 13A). 15
 Dorsal plates covered by delicate cuticular droplets; setae
 in dorsal membranous cuticle longer than OC
 *H. psammophilus* Bartsch, 1993a
15. Pore canaliculus on the OC slightly posterior to glp-3;
 both ventral spines on telofemur I inserted close to the
 distal margin of the segment; anterior margin of female
 PD closer to ds-4 than to ds-5
 *H. mitrellus* Bartsch, 1993a
 Pore canaliculus on the OC distinctly anterior to glp-3;
 one of the two ventral spines on telofemur I in proximal
 half; anterior margin of female PD much closer to ds-5
 than to ds-4 *H. rarus* sp. nov.

ACKNOWLEDGEMENTS

I thank the Australian Biological Resources Study for funding, the Australian Institute of Marine Science for providing facilities, the Great Barrier Reef Marine Park Authority for collecting permits, and Manfred Grasshoff, Mark

Harvey, Mark Judson and Ulrike Schreiber for the loan of material. I acknowledge Ilse Bartsch for comments on the manuscript and Carolina Bastidas, Sue Codi, Greg Coleman, Guillermo Diaz-Pulido, Katharina Fabricius, Angus Thompson, Paula Tomkins and Sven Uthicke for collection of specimens. This publication is contribution no. 1017 of the Australian Institute of Marine Science.

LITERATURE CITED

- BARTSCH, I. 1972. Ein Beitrag zur Systematik, Biologie und Ökologie der Halacaridae (Acari) aus dem Litoral der Nordund Ostsee. I. Systematik und Biologie. Abhandlungen und Verhandlungen des naturwissenschaftlichen Vereins in Hamburg (NF) 16: 155-230.
1974. *Agaua vajeta* n. sp., Beschreibung einer Halacaride (Acari) von Südafrika. Revue de Zoologie Africaine 88: 175-179.
1979. Halacaridae (Acari) aus der Bucht von Morlaix (Bretagne). Acarologia 21: 34-45.
1981. Halacaridae (Acari) aus dem Kanal von Moçambique. Cahiers de Biologie Marine 22: 35-63.
1983. Vorschlag zur Neugliederung des Systems der Halacaridae (Acari). Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere 110: 179-200.
1984. Halacaridae (Acari) von den westindischen Inseln. Bijdragen tot de Dierkunde 54: 185-196.
1985. New species of Halacaridae (Acari) from New Zealand. New Zealand Journal of Zoology 12: 547-560.
1990. Antarctic Halacaroida (Acari): genera *Agaua*, *Bradyagaue*, and *Halacarellus*. Antarctic Research Series 52: 185-217.
1992. Halacariden von den Inseln Moorea und Bora Bora, Gesellschaftsinseln, Polynesien (Arachnida: Acari). Senckenbergiana biologica 72: 465-488.
- 1993a. *Halacarus* (Halacaridae, Acari) from south-western Australia. Pp. 19-43. In Wells, F.E., Walker, D.I., Kirkman, H. & Lethbridge R. (eds) The Marine Flora and Fauna of Rottnest Island, Western Australia, Volume 1. (Western Australian Museum: Perth).
- 1993b. *Halacarus malaysius*, a new halacarid mite (Halacaridae: Acari) from the island of Babi Besar, Peninsular Malaysia. Raffles Bulletin of Zoology 41: 297-302.
- 1993c. Synopsis of the Antarctic Halacaroida (Acari). (Koeltz Scientific Books: Koenigstein).
1997. *Thalassarachna* and *Halacarellus* (Halacaridae: Acari): two separate genera. Journal of Natural History 31: 1223-1236.
1998. Halacarinae (Acari: Halacaroida) from the northwestern Black Sea: a review. Mitteilungen aus dem hamburgischen zoologischen Museum und Institut 95: 143-178.

- 1999a. Halacaridae (Acari) from Rottnest Island, Western Australia. Mites on fronds of the seagrass *Amphibolis*. Pp. 333-357. In Walker, D. I. & Wells, F. E. (eds) The seagrass flora and fauna of Rottnest Island, Western Australia. (Western Australian Museum: Perth).
- 1999b. *Peregrinacarus reticulatus* gen. nov. spec. nov., a freshwater halacarid mite (Acari, Halacaridae) from Marion Island. *Hydrobiologia* 392: 225-232.
2000. Rhombognathinae (Acari: Halacaridae) from the Great Barrier Reef, Australia. *Memoirs of the Queensland Museum* 45: 165-203.
- BARTSCH, I. & PUGH, P. J.A. 1994. Two new species of *Halacarellus* (Halacaridae: Acari) from South Georgia. *Journal of Natural History* 28: 493-499.
- GOSSE, P. 1855. Notes on some new or little-known marine animals (parts 2 and 3). *Annals and Magazine of Natural History* (second series) 16: 27-36, 305-306.
- GREEN, J. & MACQUITTY, M. 1987. Halacarid mites (Arachnida: Acari). *Synopses of the British Fauna* 36: 1-178.
- KRANTZ, G.W. 1973. Four new predatory species of Halacaridae (Acari: Prostigmata) from Oregon, with remarks on their distribution in the intertidal mussel habitat (Pelecypoda: Mytilidae). *Annals of the Entomological Society of America* 66: 975-985.
- LOHMANN, 1889. Die Unterfamilie der Halacaridae Murr. und die Meeresmilben der Ostsee. *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere* 4: 269-408.
1893. Die Halacarinen der Plankton-Expedition. *Ergebnisse der Plankton-Expedition der Humboldt-Stiftung* 2 (G. a. b): 13-95.
1907. Die Meeresmilben der Deutschen Südpolar Expedition 1901-1903. *Deutsche Südpolar-Expedition 1901-1903*, 9 (Zool. I) 5: 361-413.
- MACQUITTY, M. 1984. The marine Halacaroidea (Acari) of California. *Journal of Natural History* 18: 527-554.
- NEWELL, I.M. 1945. The status of *Thalassarachna verrilli* Packard 1871, *Halacarus* Gosse 1885, and *Copidognathus* Trouessart 1888 (Acari, Halacaridae). *Transactions of the American Microscopical Society* 64: 58-62.
1984. Antarctic Halacaroidea. *Antarctic Research Series* 40: 1-284.
- OTTO, J.C. 1994. New species of Halacaridae from Australia (Acarina: Prostigmata). *Acarologia* 35: 31-48.
- 1999a. The halacarid fauna of the Great Barrier Reef and Queensland Plateau: the genera *Agauopsis* and *Halacaropsis* (Acarina: Halacaridae). *Memoirs of the Queensland Museum* 43: 797-817.
- 1999b. Four new species of *Agau* (Acarina: Halacaridae) from the Great Barrier Reef Marine Park. *Cahiers de Biologie Marine* 40: 273-281.
- 1999c. *Corallihalacarus chilcottensis*, a new genus and species of marine mite from the Queensland Plateau (Acarina: Halacaridae). *Zoological Science* 16: 839-843.
- 2000a. Simognathinae (Acarina: Halacaridae) from the Great Barrier Reef and Queensland Plateau, description of thirteen new species. *Memoirs of the Queensland Museum* 45: 505-534.
- 2000b. Halacaridae from the Great Barrier Reef and Queensland Plateau: the genera *Lohmannella*, *Scaptognathides* and *Scaptognathus* (Acarina: Halacaridae: Lohmannellinae). *Memoirs of the Queensland Museum* 45: 535-555.
- 2000c. Six closely related species of the *Copidognathus gibbus* group (Acarina: Halacaridae) from northeastern Australia. *Cahiers de Biologie Marine* 41: 223-232.
- 2000d. *Australacarus* (Acari: Halacaridae) from northern Australia, with the description of three new species. *Records of the Western Australian Museum* 20: 103-114.
- 2000e. *Acarochelopodia* and *Actacarus* species (Acari: Halacaridae) from Australia, with remarks on *A. pacificus* and *A. orthotectus*. *Species Diversity* 5: 111-127.
- 2000f. Seven new species of *Arhodeoporus* (Acarina: Halacaridae) from the Great Barrier Reef and Queensland Plateau. *Hydrobiologia* 436: 1-16.
- 2000g. *Spongihalacarus longiscutus* n. gen., n. sp., a marine mite (Acari: Prostigmata: Halacaridae) associated with an alga-sponge symbiosis from the Great Barrier Reef lagoon in Australia. *International Journal of Acarology* 26: 279-283.
- 2000h. *Xenohalacarus longirostris* n. gen., n. sp., a marine mite (Acari: Halacaridae: Lohmannellinae) from Chilcott Islet, Australia. *International Journal of Acarology* 26: 285-291.
- OTTO, J.C. & BARTSCH, I. 2000. *Tropihalacarus spio*, a new genus and species of Halacaridae (Acarina: Prostigmata) from the Great Barrier Reef. *Acarologia* 40: 171-178.
- PACKARD, A.S. 1871. On insects inhabiting salt water. *American Journal of Science* 1: 100-110.
- TROUESSART, E. 1889. Revue synoptique de la famille des Halacaridae. *Bulletin Scientifique de la France et de la Belgique* 20: 225-251.
- VIETS, K. 1927. Die Halacaridae der Nordsee. *Zeitschrift für Wissenschaftliche Zoologie* 130: 83-173.
1940. Die Meeresmilben aus der Adria (Halacaridae und Hydrachnellae, Acari). *Archiv für Naturgeschichte* (N. F.) 9: 1-135.
1952. Nachträge zu Die Meeresmilben (Halacaridae, Acari) der Fauna Antarctica. *Further Zoological Results of the Swedish Antarctic Expedition 1901-1903*, 4: 1-11.

HALACARIDAE OF THE GREAT BARRIER REEF LAGOON AND CORAL SEA: THE *COPIDOGNATHUS ORNATUS* GROUP (ACARINA: PROSTIGMATA: HALACARIDAE)

JÜRGEN C. OTTO

Otto, J.C. 2001 06 30: Halacaridae of the Great Barrier Reef Lagoon and Coral Sea: the *Copidognathus ornatus* group (Acarina: Prostigmata: Halacaridae). *Memoirs of the Queensland Museum* 46(2): 717-731. Brisbane. ISSN 0079-8835.

Seven species of the *Copidognathus ornatus* group are recorded from coral reefs in the Coral Sea and the Great Barrier Reef lagoon, among them *Copidognathus ornatus* Bartsch, a species previously known only from the Moçambique channel, and *C. hawaiiensis* Bartsch, previously described from Hawaii. The other species, *C. adonis*, *C. barrierensis*, *C. emblematus*, *C. insularis*, *C. orarius* and *C. prideauxae*, are new to science. These represent the first record of the *ornatus* group from Australia. A key to species of the *ornatus* group is presented. □ *Copidognathus*, Great Barrier Reef, Halacaridae, Acarina.

Jürgen C. Otto Australian Institute of Marine Science, PMB 3, Townsville 4810, Australia (e-mail j.otto@aims.gov.au); 3 October 2000.

Among the predominantly marine mite family Halacaridae, *Copidognathus*, with over 300 known species, accounts for almost one third of all known species. Although cosmopolitan, *Copidognathus* reaches its highest diversity in tropical or subtropical waters where it is known to constitute up to 50% of the halacarid fauna (Bartsch, 1992). Many *Copidognathus* species have been assigned to species groups, of which the *ornatus* group (Bartsch, 1992, 1997) is one. It was previously known from only 4 species, *C. acanthoscelus* Bartsch, 1992, and *C. umbonatus* Bartsch, 1992, both from Hong Kong, *C. hawaiiensis* Bartsch, 1989, from Hawaii, and *C. ornatus* Bartsch, 1981, from the Moçambique Channel. That no species of this group were previously recorded from Australia can be attributed to the scarcity of halacarid collections along the tropical Australian coast. As the present paper shows, at least 7 species of the *ornatus* group are present in northeastern Australia.

METHODS

All material was collected by the author except where stated otherwise. Mites were cleared in lactic acid and mounted in PVA. Drawings were made with the aid of a camera lucida from compressed specimens. Abbreviations in descriptions: AD, anterior dorsal plate; AE, anterior epimeral plate; ds-1 to ds-6, dorsal idiosomal setae (excluding those on posterior epimeral plate) numbered in sequence from anterior to posterior; GA, genitoanal plate; glp-1 to glp-4, dorsal gland pores numbered in sequence from anterior to posterior; OC, ocular plate; PD, posterior dorsal plate; PE, posterior

epimeral plate; P-2, P-3, P-4, second, third and fourth palp segments, respectively, counted from base of palp; sgs, subgenital seta(e); I-IV, leg I to leg IV. Additional abbreviations used in the illustrations are explained in the captions. All specimens with an accession number prefix QMS are deposited in the Queensland Museum's branch Museum of Tropical Queensland in Townsville. Other depositories: ANIC, Australian National Insect Collection, Canberra (Australia); ZMH, Zoologisches Institut und Zoologisches Museum, Universität Hamburg (Germany).

SYSTEMATICS

Superfamily HALACAROIDEA Cunliffe, 1955
Family HALACARIDAE Murray, 1877

Copidognathus ornatus group

DIAGNOSIS. AD at least as wide as long; anteriorly developed into a short nose (Fig. 1); with one anterior and 2 posterior areolae consisting of pits that are surrounded in deeper cuticular layers by a ring of canaliculi (= rosette pores, Newell, 1947, fig. 205). OC with distinct posterior narrow tail; posterior to ds-2 with oblong medial areola. PD with pair of medial and pair of lateral costae, both pairs furnished with rosette pores except in *C. barrierensis* where only the medial pair carries rosette pores and the lateral costae are transformed into narrow non-porous ridges (Fig. 3A); posteriorly with glp-3 and glp-4. Palp segment P-2 lacking ventral cuticular spine. Legs with ventrolateral lamella or cuticular spines on telofemur (Fig. 2A-D); genu IV with 4 setae; telofemur IV without

ventral seta; tibiae I and III each with a bipectinate seta, tibia II with 2 and tibia IV either with none or one such seta.

DESCRIPTION (characters listed under diagnosis are omitted). Dorsal and ventral plates well developed (Fig. 1A). AD anterolaterally with pair of glp-1; ds-1 inserted on anteromedial margins of posterior areolae. OC anterolaterally with glp-2 at level of ds-2 or slightly anterior to ds-2, often obscured amidst a group of rosette pores (= lateral areola) that extends to the pore canaliculus on the lateral margin (Fig. 1F). PD distinctly longer than half of idiosoma; cuticle outside costae furnished with shallow pits, which in most species are arranged in groups that are separated by cuticular bars that form a reticulated pattern; medial costae slightly widened near glp-3; ds-3 on or near the anterolateral edge of plate; ds-4 anterior and ds-5 posterior to glp-3; distance between glp-3 and ds-5 less than between glp-3 and ds-4; ds-6 near posterior margin of plate. AE furnished with pits (Fig. 1B, right half), which are more or less clearly arranged within polygons and in deeper cuticular layers separate into minute canaliculi (Fig. 1B, left half); pair of epimeral pores and 3 pairs of setae; posterior margin usually concave (Fig. 1C), sometimes straight. PE with one dorsolateral and 3 ventral setae; anterior to leg III and leg IV insertions with ventrolateral rosette pore areola. GA with rosette pores posterolaterally, remainder of plate pitted. Female with 3 pairs of perigenital setae and one pair subgenital setae (Fig. 1H). Male with 4 subgenital setae, the anterior 2 pairs more delicate than the posterior 2 pairs (Fig. 1C). Rostrum gradually narrowing towards anterior (Fig. 1D), as long as or slightly shorter than gnathosomal base; one pair of maxillary setae at the gnathosomal base/rostrum interface, the other pair in anterior half of rostrum; gnathosomal base on either side with pitted areola, pits separating into canaliculi in deeper cuticular layers. Palp 4-segmented, slender; P-2 with one dorsal seta; P-3 lacking setae; P-4 with 3 setae in basal whorl. Legs shorter than idiosoma; chaetotaxy (trochanter - tibia): I 1-2-5-4-7, II 1-2-5-4-7, III 1-2-2-3-5, IV 0-2-2-4-5. Tarsus I with 3 ventral setae, the other tarsi without ventral setae (ventral pambulacral setae not counted). Tarsi I and II with solenidion in dorsolateral position. Paired claws on tarsus I smaller than on other tarsi. Empodial claw on tarsus I more clearly visible than those on other tarsi, which are either barely visible or absent. Paired claws on tarsus I smooth

or with inconspicuous pecten, those on other legs more conspicuously pectinate (Fig. 2E).

REMARKS. Species that are somewhat similar to the *ornatus* group and possibly related are *C. costipora* Newell, 1984, *C. triareolatus* Newell, 1984, *C. tuberosus* Newell, 1984 and *C. ganglionatus* Newell, 1984. However, unlike the *ornatus* group, they have a ventral seta on telofemur IV and lack a distinct tail on the ocular plates and are therefore excluded.

***Copidognathus adonis* sp. nov.**
(Figs 1,2)

ETYMOLOGY. Latin, Greek, *adonis* = a beautiful youth beloved by Venus.

MATERIAL. HOLOTYPE: QMS105673, ♂, Coral Sea, Chilcott Islet, 16°56.51'S 150°00.4'E, 14 Sep. 1998, G.A. Diaz-Pulido, coarse sand at 1-14m. PARATYPES: Coral Sea: QMS105674 (1 ♂), QMS105675 (1 ♀), ANIC (1 ♀), ZMH (1 ♀), data as for holotype; QMS105676 (1 ♂), Willis Islet, ca. 16°18'S 149°58'E, 15 Sep. 1998, G.A. Diaz-Pulido, fine to medium coarse sand at 0-10m; QMS105677-105681 (5 ♀s), QMS105682-105685 (4 ♂s), ANIC (1 ♂), ZMH (1 ♂), Lihou Reef, ca. 17°25'S 151°40'E 22 July 1998, D. Fenner, sand at 7m; QMS105686 (1 ♀), Flinders Reef, ca. 17°43'S 148°26'E, July 1998, D. Fenner, sand; QMS105687/105688 (2 ♀s), North Flinders Reefs, East Ribbon Reef, 17°41.16'S 148°33.04'E, 3 July 1999, J.C. Otto, coarse sand at 10m; QMS105689 (1 ♀), QMS 105690 (1 ♂), Flinders Reef, near cay, 17°42.73'S 148°26.29'E, 2 Jul. 1999, coarse sand at 3m; QMS105691 (1 ♀), Flinders Reef, near cay, 17°42.73'S 148°26.29'E, 2 July 1999, A. Burja, coarse sand at 5m.

DESCRIPTION. *Male and Female.* Male idiosoma 320-352µm (holotype 323µm) long, female idiosoma 326-346µm long. AD with anterior areola more slender than the 2 posterior ones, the posterior areola not extending to glp-1 (Fig. 1A). OC with medial areola consisting of at least eight rosette pores (Fig. 1F,G), often with a gap posteriorly (Fig. 1E), not extending to lateral margin of plate; between lateral and medial areolae with faint reticulate ornamentation (Fig. 1E). PD with medial and lateral costae, all separated from each other anteriorly; lateral costae sometimes with gaps interrupting the line of rosette pores; medial costae on average 2 to 3 rosette pores wide, lateral costae usually one rosette pore, posteriorly in some places 2 rosette pores wide; reticulate ornamentation between costae becoming fainter towards posterior margin; glp-3 and glp-4 associated with medial costae; ds-4 in anterior half of plate. AE with concave posterior margin. PE with a group or

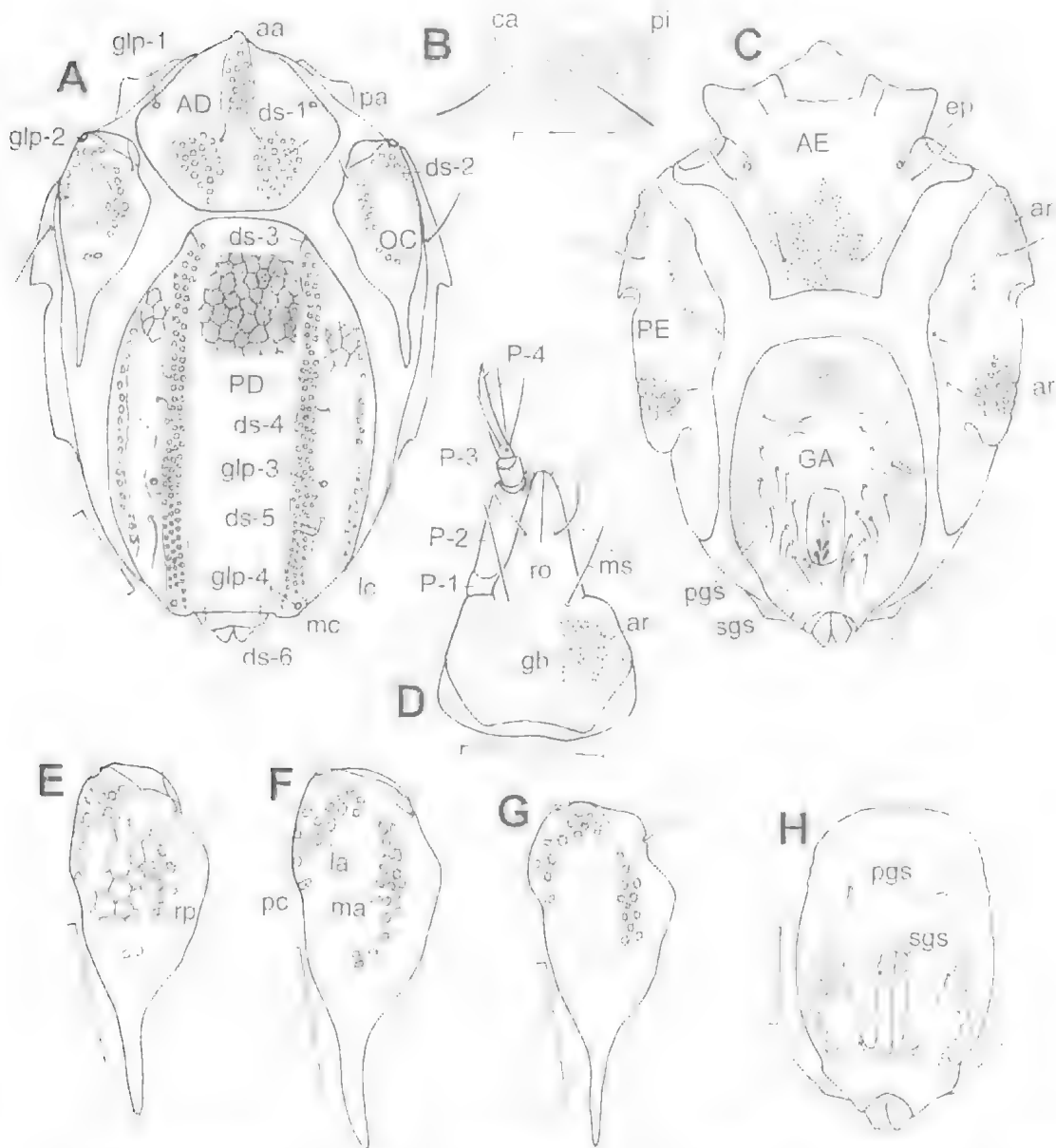


FIG. 1. *Copidognathus adonis* sp. nov., ♂. A, idiosoma, dorsal view; B, detail of anterior epimeral plate and posterior pair of setae; C, idiosoma, ventral view; D, gnathosoma, ventral view; E-G, left ocular plate in 3 specimens; H, ♂ genitoanal plate. Abbreviations: aa, anterior areola; AD, anterior dorsal plate; AE, anterior epimeral plate; ar, areola; ca, canaliculi; ds-1 to ds-6, dorsal setae 1 to 6; ep, epimeral pore; gh, gnathosomal base; glp-1 to glp-4, gland pores 1 to 4; la, lateral areola; lc, lateral costa; ma, medial areola; mc, medial costa; ms, maxillary setae; OC, ocular plate; pa, posterior areola; pc, pore canaliculus; PD, posterior dorsal plate; PE, posterior epimeral plate; pgs, perigenital seta; pi, pits; P-1 to P-4, palp segments 1 to 4; ro, rostrum; rp, rosette pore; sgs, subgenital seta. Scale bars: A, C, D-H = 50µm; B = 25µm.

band of shallow pits in the anterior half from about the inner-most seta, this group not contiguous with anterolateral areola; posterior to leg IV insertions without canaliculi. Male with

27-30 perigenital setae. Gnathosoma as depicted in Fig. 1D. Ventrolateral lamellae on telofemora elaborate (Fig. 2A-D), with smooth or slightly undulate edge. Ventral margin of tibia I lacking a

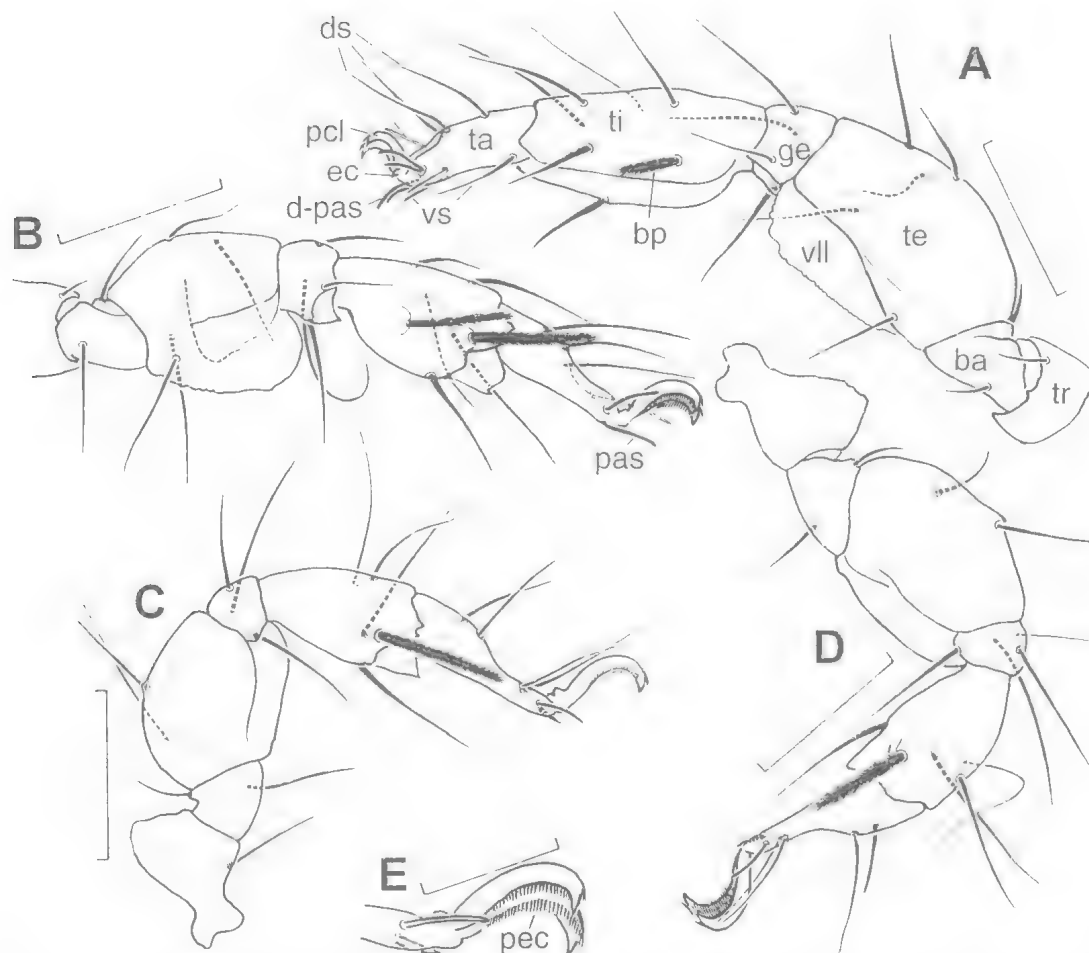


FIG. 2. *Copidognathus adonis* sp. nov., ♂; A, leg I, medial view; B, leg II, medial view; C, leg III, medial view; D, leg IV, medial view; E, claws of tarsus III, medial view. Abbreviations: ba, basifemur; bp, bipectinate seta; ds, dorsal setae; d-pas, doubled parambulacral seta; ec, empodial claw; ge, genu; pas, parambulacral seta; pcl, paired claw; pec, pecten; ta, tarsus; te, telofemur; ti, tibia; tr, trochanter; vs, ventral setae; vll, ventrolateral lamella; ω, solenidion. Scale bars: A-D = 50 μm, E = 25 μm.

conspicuous cuticular protuberance. Tibia IV with bipectinate seta. Bipectinate seta on tibia I as finely pectinate as those on other tibiae and not distinctly heavier than these. Tarsi III and IV each with 4 dorsal setae. Paired claws on tarsi II-IV with relatively fine pecten extending along the inside of the entire shaft (Fig. 2E, compare with Fig. 12E). Empodial claws on tarsi II-IV not clearly seen.

REMARKS. Other species of the *ornatus* group that have 4 setae on each of tarsi III and IV are *barrierensis*, *emblematus*, *orarius*, *ornatus* and *prideauxae*, all of which are described below.

***Copidognathus barrierensis* sp. nov.**
(Figs 3,4)

ETYMOLOGY. From the Great Barrier Reef.

MATERIAL. HOLOTYPE: QMS105731, ♂, GBR, No Name Reef, ca. 14°39'S 145°40'E, 9 Oct. 1998, medium coarse sand at 6m. PARATYPES: GBR: QMS105732 (1 ♂), data as for holotype; QMS105692 (1 ♀), QMS105695 (1 ♀), QMS105693/ 105694 (2 ♂s), Loadstone Reef, 18°41.91'S 147°06.49'E, 12 Apr. 1998, sand & rubble at 2m; ANIC (1 ♀), ZMH (1 ♀), Loadstone Reef, 18°42.03'S 147°06.54'E, 12 Apr 1998, coarse sand & rubble at 12-15m; ZMH (1 ♂), ANIC (1 ♂), Loadstone Reef, 18°42.05'S 147°05.98'E, 12 Apr. 1998, coarse sand & rubble at 8m; QMS105696-105699 (4 ♀s), Faraday Reef, 18°25.93'S 147°21.11'E, 13 Apr. 1998, coarse sand

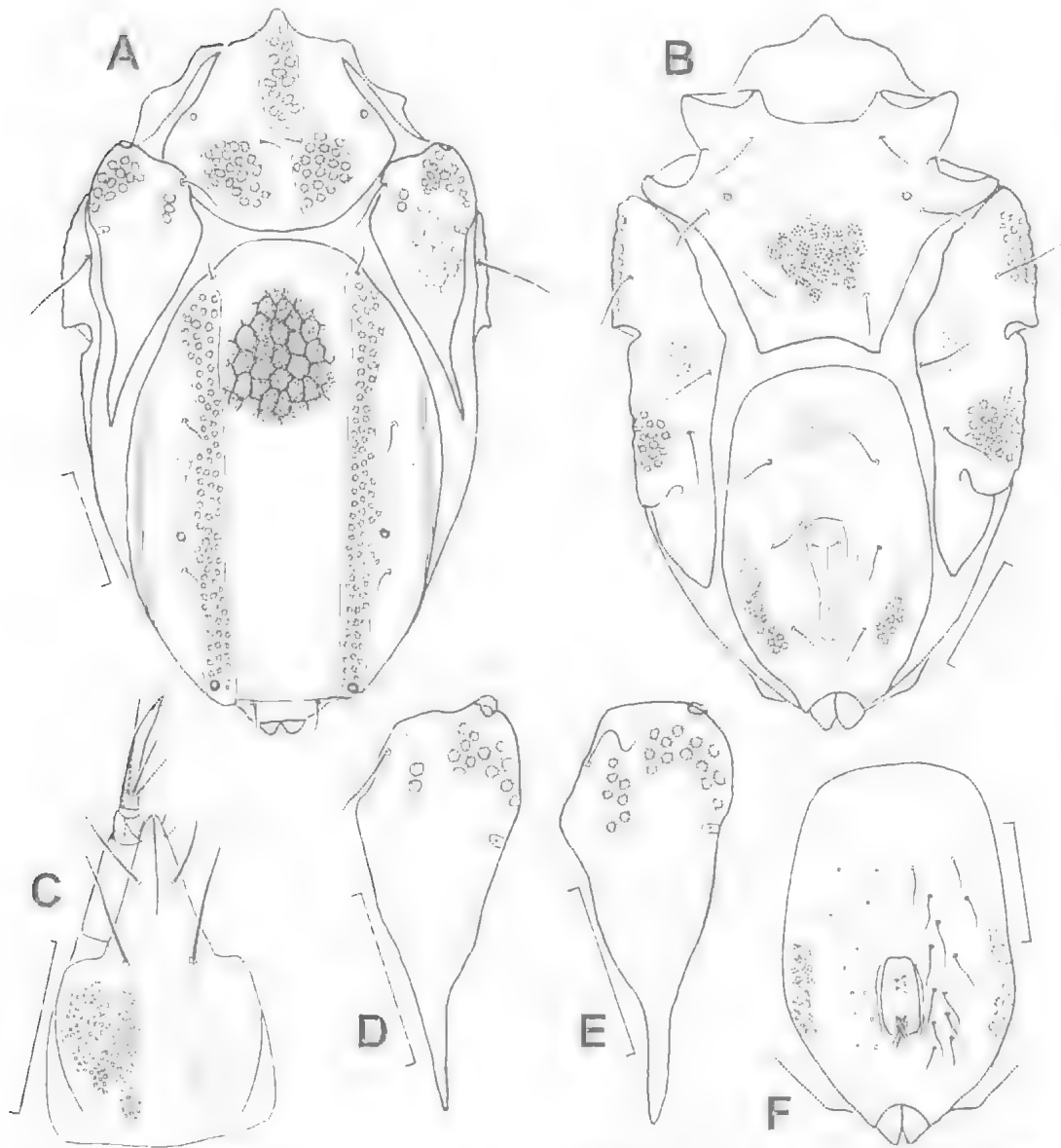


FIG. 3. *Copidognathus barrierensis* sp. nov.; A, ♀, idiosoma, dorsal view; B, ♀, idiosoma, ventral view; C, gnathosoma, ♀, ventral view; D, E, ocular plate of ♀s; F, ♂, genitoanal plate. Scale bars: A–F = 50 µm.

& rubble at 6–9 m; QMS105700 (1 ♂), QMS105701 (1 ♀), Bramble Reef, 18°25.25'S 146°40.65'E, 10 Apr. 1998, medium coarse sand at 3–6 m; QMS105702 (1 ♂), QMS105703 (1 ♀), Bramble Reef, 18°26.36'S 146°42.24'E, 9 Apr. 1998, coarse sand at 5 m; QMS105704 (1 ♂), Turner Cay, NE, ca. 21°43'S 152°33'E, 8 Dec. 1998, medium coarse sand at 3 m; QMS105705 (1 ♀), Howard Patch, ca. 22°23.5'S 152°37'E, 6 July 1998, D. Fenner, sand at 6 m; QMS105706 (1 ♀), 23°12.22'S 151°58.49'E, 27 Aug. 1999, coarse sand at 60 m, I. Zagorskis; QMS105707 (1 ♀), Myrmidon Reef, 18°16.69'S 147°23.21'E, 14 Apr. 1998, coarse sand at

12 m; QMS105708 (1 ♂), Elizabeth Reef, 19°20.12'S 149°02.85'E, 25 Dec. 1997, coarse sand & rubble at 3 m; QMS105709 (1 ♂), Faraday Reef, 18°24.87'S 142°20.79'E, 12 Apr. 1998, on sponge at 10 m; QMS105710–105711 (2 ♀s), Lavers Cay, 21°13'S 151°59'E, 20 Apr. 1999, chunks of coral rubble just above low tide mark, sediment depth 0–10 cm; QMS105712 (1 ♂), Boulder Reef, ca. 15°24'S 145°27'E, 8 Oct. 1998, A. Thompson, coarse sand at 2 m; QMS105713 (1 ♀), Lizard Island, Coconut Beach, ca. 14°40'S 145°28'E, 13 Oct. 1998, medium coarse sand at 0.5 m.

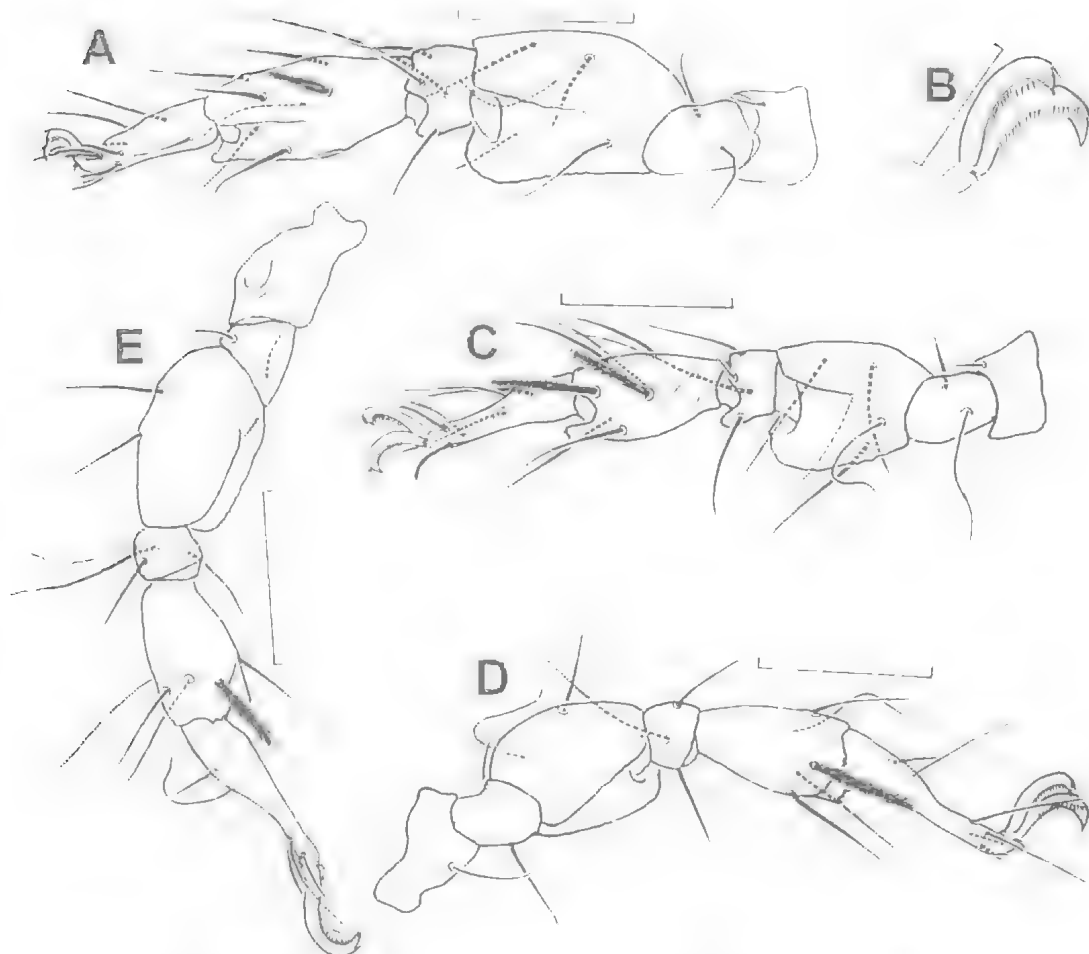


FIG. 4. *Copidognathus burrierensis* sp. nov., ♀. A, leg I, ventromedial view; B, claws on tarsus II, ventromedial view; C, leg II, ventromedial view; D, leg III, medial view; E, leg IV, medial view. Scale bars: A, C-D = 50 µm; B = 25 µm.

DESCRIPTION. *Male and Female.* Male idiosoma 313-326 µm (holotype 326 µm), female idiosoma 298-326 µm long. AD with anterior areola more slender than the 2 posterior ones; posterior areolae not extending to glp-1 (Fig. 3A). Medial arcola (Fig. 3A,D,E) on OC with usually 2-3, maximally 5 rosette pores; between lateral and medial arcola faintly reticulate. PD with pair of porous medial costae (2-3 rosette pores wide), and pair of narrow non-porous lateral costae in form of a narrow ridge; glp-3 and glp-4 associated with medial costa; ds-4 on anterior half of plate; between costae with conspicuous reticulated ornamentation that becomes fainter towards posterior. AE with concave posterior margin (Fig. 3B). PE in anterior half close to inner margin with a group or

band of shallow pits, this group or band not contiguous with the anterolateral areola. Male with 23-30 perigenital setae. Ventrolateral lamella on telofemora elaborate, with smooth or slightly undulate edges (Fig. 4A,C-E). Tibia IV with bipectinate seta. Bipectinate seta on tibia I as finely pectinate as those of other tibiae and not heavier than these. Tarsi III and IV with 4 dorsal setae. Paired claws of tarsi II-IV finely pectinate along most of shaft (Fig. 4F). Empodial claw on tarsi II-IV barely visible.

REMARKS. *Copidognathus burrierensis* can be distinguished from all other species in the *ornatus* group by having the lateral costae on the PD transformed into narrow non-porous ridges. In all other species in the group the lateral costae are furnished with rosette pores. A further

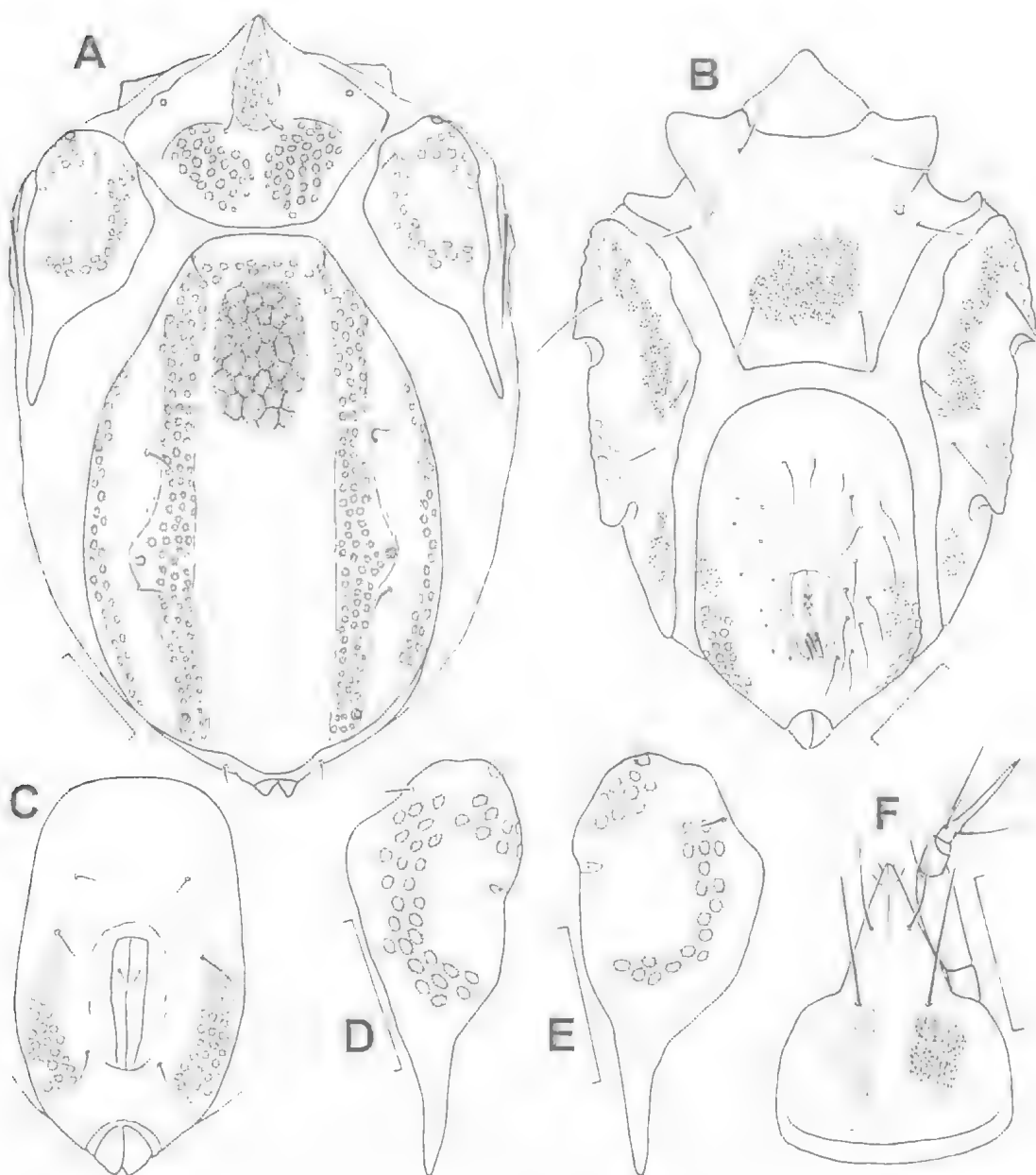


FIG. 5. *Copidognathus emblematus* sp. nov. A, ♂, idiosoma, dorsal view; B, ♂, idiosoma, ventral view; C, ♀, genitoanal plate; D, E, ocular plates in 2 ♂s; F, ♀, gnathosoma, ventral view. Scale bars: A-F = 50 µm.

character by which it can be identified is the relatively short medial areola on the OC that has fewer rosette pores than any other species in the *ornatus* group.

***Copidognathus emblematus* sp. nov.**
(Figs 5,6)

ETYMOLOGY: Greek, *emblematus* = ornament.

MATERIAL. HOLOTYPE: QMS105714, ♂, GBR, Lizard Island, Coconut Beach, ca. 14°40'S 145°28'E, 13 Oct. 1998, medium coarse sand at 0.5m. PARATYPES: Great Barrier Reef: QMS105715 (1 ♂), ANIC (1 ♂), ZMH (1 ♂), data as for holotype; QMS105716 (1 ♂), Lizard Island, Coconut Beach, ca. 14°40'S 145°28'E, 13 Oct. 1998, medium coarse sand at mid-tide level, sediment depth 10cm; QMS105717 (1 ♂), Elizabeth Reef, 19°20.12'S 149°02.85'E, 25 Dec. 1997, coarse sand &

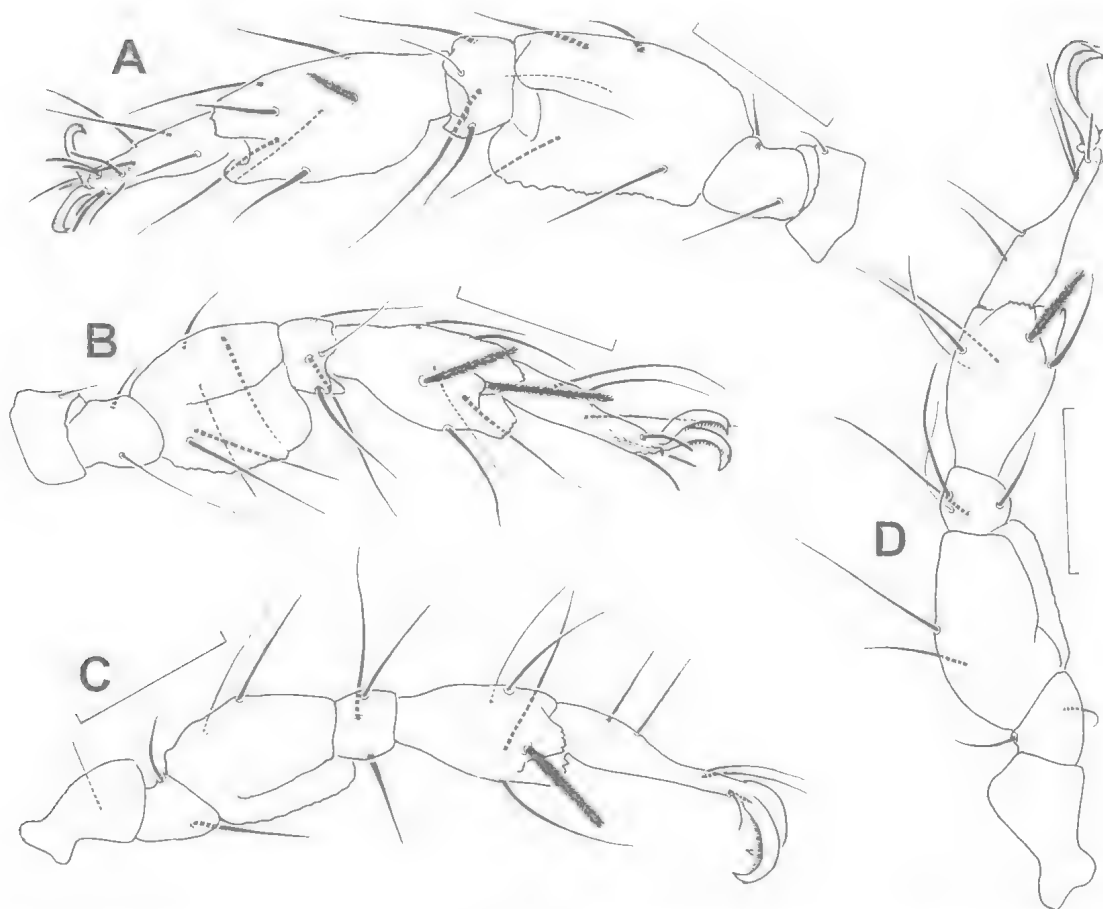


FIG. 6. *Copidognathus emblematus* sp. nov., ♂. A, leg I, ventromedial view; B, leg II, ventromedial view; C, leg III, medial view; D, leg IV, medial view. Scale bars: A-D = 50µm.

rubble at 3m; QMS105718 (1 ♂), John Brewer Reef, 18°38.25'S 147°04.42'E, 11 Apr. 1998, coarse sand at 15m; ANIC (1 ♀), ZMH (1 ♀), QMS105719-105721 (3 ♂s), East Cay, 21°29'S 152°33'E, 18 Apr. 1999, reef flat, coarse sand; QMS105722-105725 (4 ♂s), QMS105726/105727 (2 ♀s), Boulder Reef, ca. 15°24'S 145°27'E, 8 Oct. 1998, A. Thompson, coarse sand at 2m; QMS105728 (1 ♀), Reef 22-101, 21°02.5'S 151°30'E, 16 Apr. 1999, reef flat at 1m; QMS105729 (1 ♂), Turner Cay, 21°43'S 152°33'E, reef flat, 17 Apr. 1999, coarse sand at 2m.

DESCRIPTION. *Male and Female.* Male idiosoma 326-374µm long (holotype 352µm), female idiosoma 346-368µm long. AD with anterior areola more slender than the 2 posterior ones; posterior areolae not extending to glp-1. OC (Fig. 5A,D,E) with medial areola consisting of at least 15 rosette pores; both areolae in some specimens barely separated (Fig. 5D); between areolae with faint reticulate ornamentation. PD

with pair of medial and pair of lateral costae, medial costae 2-3 rosette pore wide, lateral costae 1-2 rosette pore wide; medial costae either connected anteriorly by a transverse band of rosette pores (variable width between specimens, in some specimens only one rosette pore, in others 2-3 rosette pores wide) or both costae completely separate; between costae with reticulated ornamentation, gradually becoming fainter towards posterior; glp-3 and glp-4 associated with medial costae; ds-4 on anterior half of plate. AE with slightly concave posterior margin. PE in anterior half close to inner margin with a band of pits and underlying canaliculi that is contiguous with the anterolateral rosette pore areola (Fig. 5B); further groups of canaliculi posterior to insertions of leg IV. Male with 26-29 perigenital setae. Ventrolateral lamella on telofemora elaborate, with smooth or slightly undulate edges (Fig. 6A-D). Tibia IV with

bipectinate seta. Bipectinate seta on tibia I as finely pectinate as those on other tibiae and not heavier than these. Tarsi III and IV with 4 dorsal setae. Paired claws of legs II-IV finely pectinate. Empodial claws on tarsi II-IV barely visible.

REMARKS. The combination of 4 dorsal setae on tarsi III and IV and 4 porous costae on the PD is present also in *C. adonis*, *C. prideauxae* and *C. ornatus*, all of which are described below. *Copidognathus emblematus* can be distinguished from *C. adonis* by having groups of canaliculi on the PE posterior to leg IV insertions and by having a broad band of pits and underlying canaliculi arising from anteromedial areola on the PE. A group or band of shallow pits in the anterior half of the PE is also present in *C. adonis*. However, in the latter species, these are not contiguous with the anterior rosette pore areola on the PE, as is the case in *C. emblematus*. A further difference between both species is in the ornamentation along the anterior margin of the PD. In *C. emblematus* a transverse band of rosette pores connecting both medial costae anteriorly was found in some but not all specimens, while in *C. adonis* it was absent in all specimens. It follows that presence of a transverse band identifies *C. emblematus* while absence of a transverse band is inconclusive. It is interesting to note that the transverse band was absent only in *C. emblematus* specimens collected on the most southerly sites, south of 21°S (East Cay, Reef 22-101, Turner Cay).

Differences between *C. emblematus*, *C. orarius* and *C. prideauxae* are discussed under the remarks to the latter species.

***Copidognathus hawaiiensis* Bartsch, 1989**
(Figs 7,8)

Copidognathus hawaiiensis Bartsch, 1989: 141.

MATERIAL. Australia, GBR: QMS105742 (1 ♀), Morris Island, 13°29'S 143°44'E, 18 Aug. 1999, C. Bastidas, K. Fabricius & S. Uthicke, fine- medium coarse sand; QMS105743 (1 ♂), Whitsunday Islands, Long Island, ca. 20°23'S 148°52'E, 28 Feb. 1997, sand at 0.5 m. Indonesia, Bali: QMS105744 (1 ♂), QMS105745 (1 ♀), Menjangan Island, 9 Mar. 1999, J. Benzie, coarse-fine sand in 0.3-0.5m water depth.

DESCRIPTION. *Male and Female* (listed material only). Idiosoma in Australian and Indonesian males 352µm and 314µm, respectively, in Australian and Indonesian females 314µm and 310µm, respectively. AD with posterior areolae extending to glp-1; along posterior margin with a band of rosette pores

(Fig. 7A). Medial areola on OC with at least 11 rosette pores; remainder of plate with scattered shallow pits. PD with 2-4 rosette pore wide medial and lateral costae, all connected anteriorly; no reticulation seen between costae. Pores glp-3 in lateral costa, glp-4 in medial costa; ds-4 in anterior half of plate. AE with straight or concave posterior margin (Fig. 7B); PE with rosette pores posterior to leg IV insertions. Male with ca. 20-24 perigenital setae. Telfemur I with ventrolateral lamella transformed into 2 conspicuous protuberances (Fig. 8A), on one side of a specimen with an additional protuberance (Fig. 8E); a cuticular spine distally on medial flank. Tibia I with one ventral and one smaller distomedial protuberance, each associated with a seta. Telfemur I conspicuously pitted on lateral flank (Fig. 8F). Tibia IV with bipectinate seta. Bipectinate seta on tibia I more robust than those on other segments. Tarsi III and IV with 3 dorsal setae. Empodial claw on tarsi II-IV clearly visible. Paired claws of tarsus I smooth, those on tarsi II-IV with moderately coarse pecten over most of the shaft.

REMARKS. I have been unable to find any taxonomically important differences between the Hawaiian type and the Australian or Indonesian material listed above, and conclude that these are conspecific. Thus, *C. hawaiiensis* is the third halacarid species that is known to occur in Hawaii as well as the Great Barrier Reef. The other 2 are *Acarochelopodia biunguis* Bartsch (Otto, 2000b) and *Scaptognathus kunzi* Bartsch (Otto, 2000a). The common occurrence of these species on both the Hawaiian archipelago and the Great Barrier Reef is noteworthy, as Halacaridae in general have poor dispersal ability and areas that are separated by large and deep bodies of water therefore usually have different halacarid faunas.

C. hawaiiensis is similar to *C. acanthoscelus* Bartsch, 1992, in having the ventrolateral lamella on telfemur I transformed into spines and in having a conspicuous ventral protuberance on tibia I that is associated with a seta. *C. acanthoscelus* differs from *C. hawaiiensis* in that the spines on telfemur I are more numerous and in the glp-3 being associated with the medial instead of the lateral costae on the PD.

***Copidognathus orarius* sp. nov.**
(Figs 9,10)

ETYMOLOGY. Latin, *orarius* = of the coast.

MATERIAL. HOLOTYPE: QMS105735, ♂, Great Barrier Reef, Taylors Beach, near Lucinda, ca.18°37'S

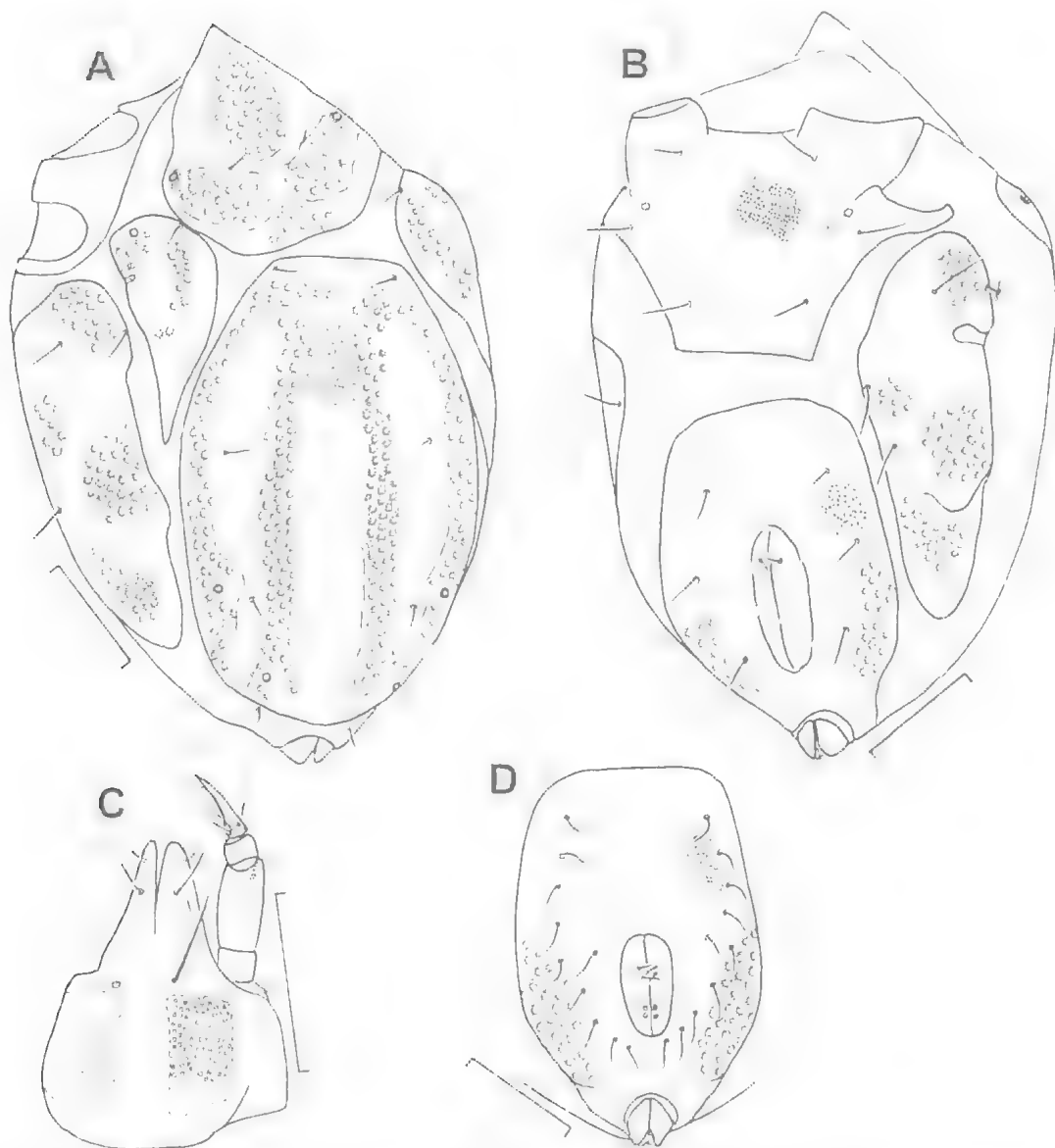


FIG. 7. *Copidognathus hawaiiensis* Bartsch; A, ♀, idiosoma, dorsolateral view; B, ♀, idiosoma, ventrolateral view; C, ♀, gnathosoma, ventral view; D, ♂, genitoanal plate. Scale bars: A-D = 50µm.

146°20'E, 14 Dec 1997, medium coarse sand just above low tide mark, sediment depth 0-5cm. PARATYPES: ANIC (1 ♀), ZMH (1 ♀), QMS105733/105734 (2 ♀s), ANIC (1 ♂), ZMH (1 ♀), QMS105736-05740 (5 ♂s), data as for holotype. OTHER MATERIAL: QMS105741 (1 ♂), Indonesia, Bali, Menjangan Island, 9 Mar., 1999, J. Benzie, coarse-fine sand in 0.3-0.5m water depth.

DESCRIPTION. *Male and Female.* Idiosoma in Australian and Indonesian males 288-307µm (holotype 307µm) long and 278µm long, respectively, in Australian females 282-304µm

long. AD with distinctly blunt nose (Fig. 9A); posterior areolae extending to glp-1; along posterior margin with band of rosette pores; cuticle between areolae with scattered pits. OC with medial areola consisting of at least 15 rosette pores and extending to lateral margin of plate; remainder of plate with scattered pits. PD with medial and lateral costae, all connected anteriorly; lateral areola on average 2 rosette pores wide; medial areola increasing in width

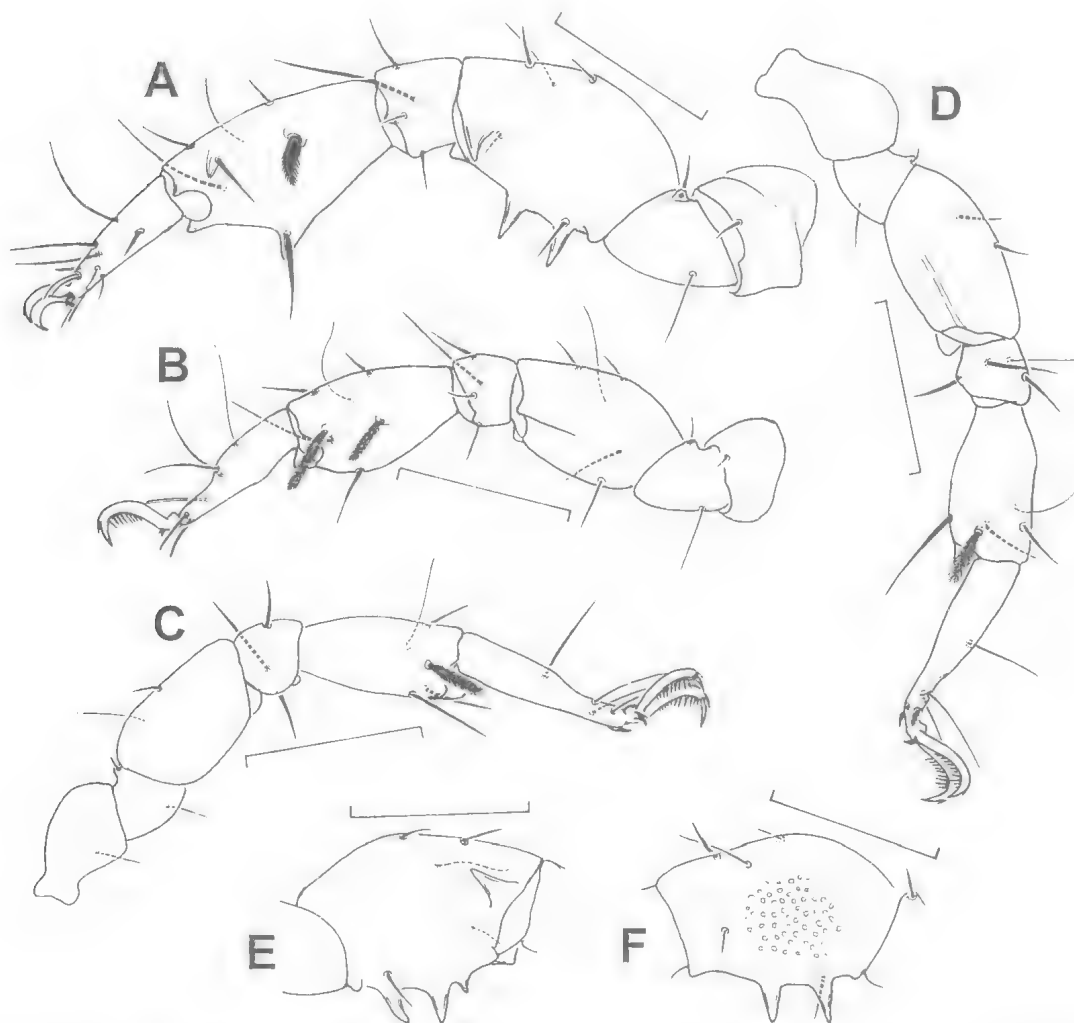


FIG. 8. *Copidognathus hawaiiensis* Bartsch, ♀; A, leg I, ventromedial view; B, leg II, medial view; C, leg III, ventromedial view; D, leg IV ventromedial view; E, telofemur I, medial view; F, telofemur I, lateral view. Scale bars: A-F = 50 µm.

towards posterior, at level of glp-3 ca. 4-5 rosette pores wide; reticulation between costae barely visible; glp-3 and glp-4 associated with medial costae; ds-4 in posterior half of plate. AE with concave posterior margin (Fig. 9B). PE in anterior half with broad band of pits and underlying canaliculi extending from about the inner-most seta to the anterior-most seta or the anterolateral rosette pore areola; posterior to leg IV insertions with canaliculi. Male with ca. 24-27 perigenital setae. Female GA as in Fig. 9D. Gnathosoma as depicted in Fig. 9C. Ventrolateral lamellae on telofemora poorly developed, with smooth edges (Fig. 10A-C,E). Tibia IV with one bipectinate seta. Bipectinate seta on tibia I

distinctly more robust than those on the other tibiae, and with coarser pectination; ventral seta on tibia I distinctly thickened and spine-like. Empodial claw on all tarsi clearly visible. Paired claws of tarsus I smooth, those on tarsi II-IV with a short cluster of about 5-7 teeth that increase in size towards the distal end of the claw; cluster of teeth discontinuous with accessory process (Fig. 10D); paired claws II-IV conspicuously slender.

REMARKS. Among the species of the *ornatus* group *C. orarius* resembles most closely *C. umbonatus*. Both species can be distinguished by the morphology of the tarsal claws. *Copidognathus orarius* has maximally 7 tines on each claw II-IV, and this short row of tines does not

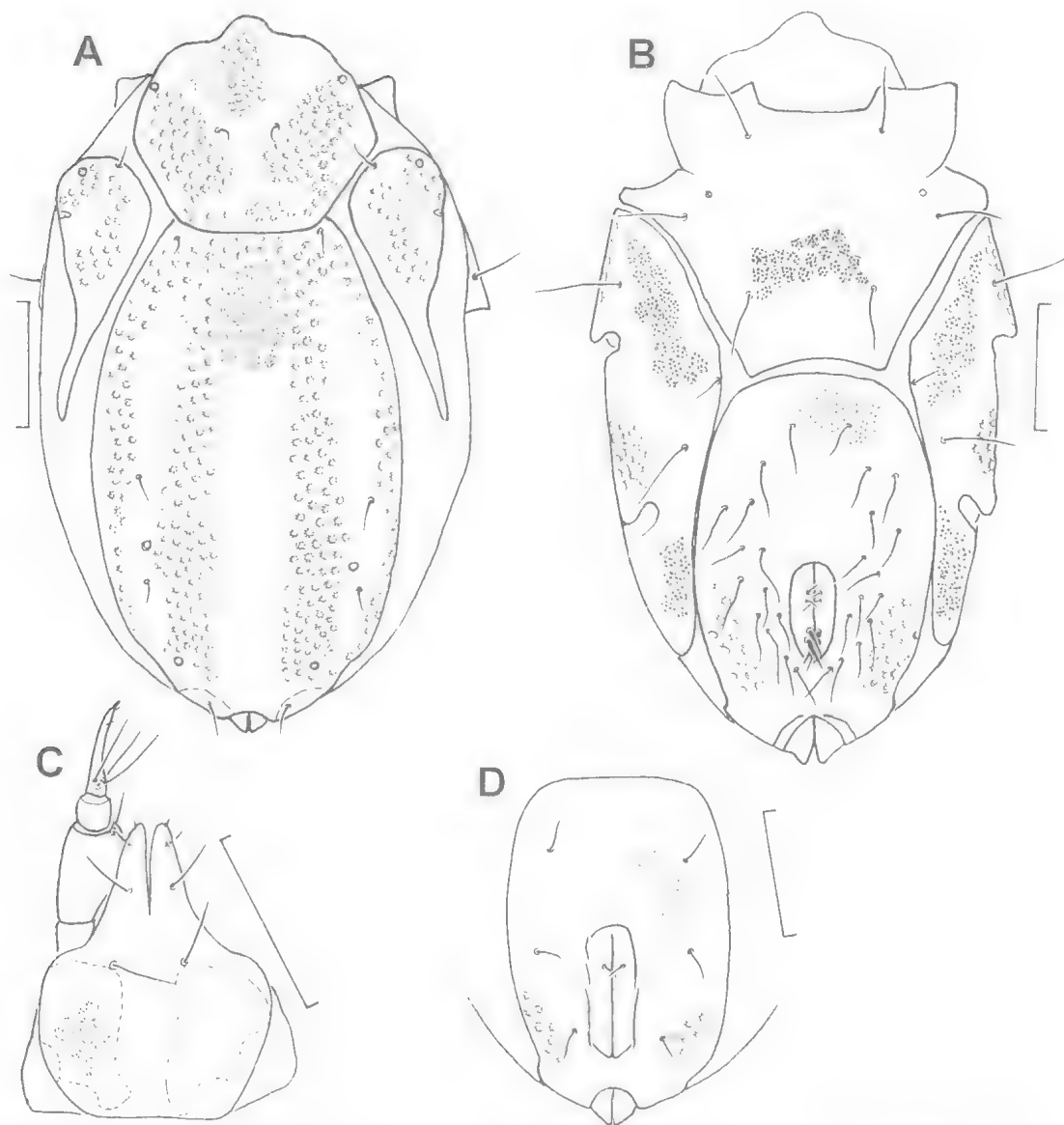


FIG. 9. *Copidognathus orarius* sp. nov.: A, ♀, idiosoma, dorsal view; B, ♂, idiosoma, ventral view; C, ♀, gnathosoma, ventral view; D, ♀, genitoanal plate. Scale bars: A-D = 50 μ m.

connect to the inconspicuous accessory process. By contrast, in *C. umbonatus* each claw II-IV has at least 12 tines and this row of tines extends along the entire apical half of the claw and merges into the accessory process.

***Copidognathus ornatus* Bartsch, 1981**

Copidognathus ornatus Bartsch, 1981: 58.

MATERIAL: QMS105730 (1 ♂), Great Barrier Reef, Whitsunday Islands, Long Island, ca. 20°23'S 148°52'E, 28 Feb. 1997, sand & coral rubble at 0.5m

The 352 μ m long specimen agrees in all aspects under examination with the holotype of *C. ornatus* from the Moçambique Channel. *C. ornatus* can be distinguished from all other species in the *ornatus* group by having 2 glabrous ventral setae on tibiae IV, instead of one bipectinate and one glabrous seta that are present in all other species.

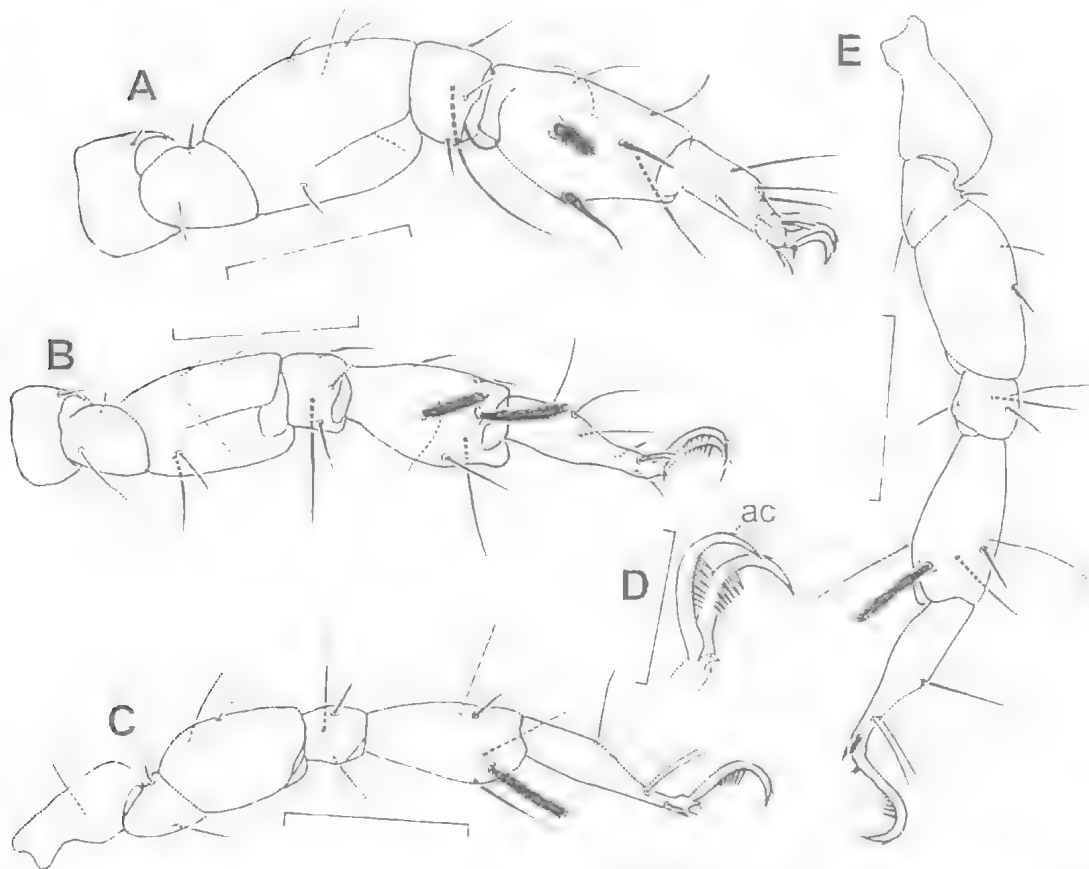


FIG. 10. *Copidognathus orarius* sp. nov.; A, ♀, leg I, ventromedial view; B, ♀, leg II, ventromedial view; C, ♀, leg III, medial view; D, ♂, detail of claws on tarsus IV, ventromedial view; E, ♀, leg IV medial view. Abbreviation: ac, accessory process. Scale bars: A-C, E = 50 µm; D = 25 µm.

***Copidognathus prideauxae* sp. nov.**
(Figs 11, 12)

ETYMOLOGY. For my friend, the late Anne Teresa Prideaux Payne.

MATERIAL. HOLOTYPE: QMS105746, ♂, Great Barrier Reef, No Name Reef, ca. 14°39'S 145°40'E, 9 Oct. 1998, medium coarse sand at 6m. PARATYPE: QMS105747 (1 ♂), data as for holotype.

DESCRIPTION. *Male.* Idiosoma 320–352 µm (holotype 320 µm) long. AD with posterior areolae not extending to glp-1 (Fig. 11A); along posterior margin with band of rosette pores. OC with medial areola consisting of at least 13 rosette pores which in holotype and paratype show a gap posteriorly. PD with both medial costae appearing clearly separated when focussing onto the canaliculi in deeper cuticular layers but appearing connected through a band of shallow

pits on the surface of the plate; medial costa about 2–3, lateral costa 1–2 rosette pores wide; between costae with reticulated ornamentation becoming fainter towards posterior; glp-3 and glp-4 associated with the medial costa; ds-4 about half way along plate. AE with concave posterior margin (Fig. 11B). PE with extensive and conspicuous band of canaliculi extending from near the inner-most seta to the anterior areola; similar canaliculi posterior to insertions of leg IV. GA with 27–33 perigenital setae. Gnathosoma (Fig. 11C). Ventrolateral lamella on telofemora with smooth or slightly undulate edge (Fig. 12A–D). Tibia I without ventrolateral cuticular protrusion. Tibia IV with bipectinate seta. Bipectinate seta on tarsus I as finely pectinate as those on other tibiae. Tarsi III and IV with 4 dorsal setae. Paired claws legs II–IV coarsely pectinate (Fig. 12E). Empodial claws on tarsi II–IV barely visible under oil immersion.

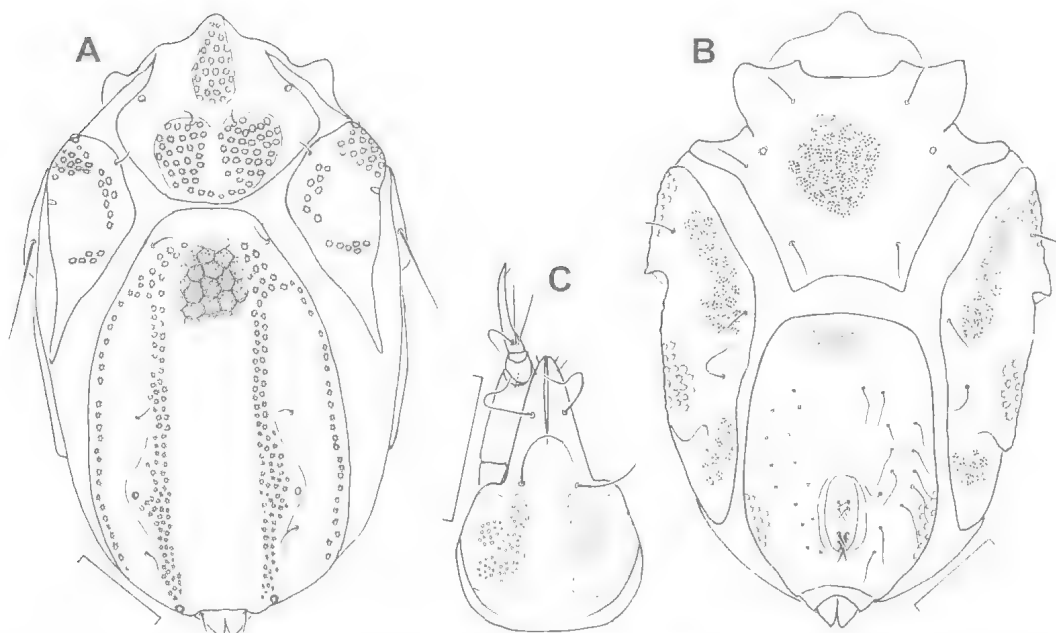


FIG. 11. *Copidognathus prideauxae* sp. nov., ♂; A, idiosoma, dorsal view; B, idiosoma, ventral view; C, gnathosoma, ventral view. Scale bars: A-C = 50 µm.

REMARKS. The only other species of the *ornatus* group with 4 setae on tarsi III and IV and similarly coarse pecten on tarsal claws II-IV is *C. ornatus* (my observation on the holotype). *C. prideauxae* differs from *C. ornatus* by having a bipectinate seta on tibia IV.

KEY TO SPECIES OF THE *COPIDOGNATHUS ORNATUS* GROUP

1. Ventrolateral lamella on telofemur I transformed into at least 2 large spines (Fig. 8A,F); tibia I with a ventral protuberance that is associated with a seta (Fig. 8a) . . . 2
 Ventrolateral lamella on telofemur I either smooth or slightly undulated (Fig. 2A), not transformed into 2 conspicuous spines; tibia I without a ventral protuberance that is associated with a seta . . . 3
2. Ventrolateral lamella on telofemur I transformed into 2 large spines, or 2 large and one much smaller spine; glp-3 in lateral areolae, more lateral than ds-5 *C. hawaiiensis* Bartsch
 Ventrolateral lamella on telofemur I transformed into more than 3 spines; glp-3 on outer edge of medial areola and directly anterior to ds-5 *C. acanthoseolus* Bartsch
3. Tarsi III and IV each with 3 dorsal setae 4
 Tarsi III and IV each with 4 dorsal setae 5
4. Paired claws on tarsi II-IV each with a short row of 5-7 teeth that is discontinuous with the accessory process *C. orarius* sp. nov.
 Paired claws on tarsi II-IV with a row of at least 12 teeth that is continuous with the accessory process *C. umbonatus* Bartsch
5. PD without lateral costae bearing rosette pores; medial areola on OC consisting of 2-5 rosette pores *C. barrierensis* sp. nov.
 PD with lateral costae bearing rosette pores; medial areola on OC consisting of at least eight rosette pores . . . 6
6. Tibia IV with a bipectinate seta (Fig. 2D), 7
 Tibia IV without a bipectinate seta *C. ornatus* Bartsch
7. Paired claws on tarsi II-IV with teeth that increase in size towards the distal end of the claw. *C. prideauxae* sp. nov.
 Paired claws on tarsi II-IV finely pectinate throughout, pectines not increasing in size towards distal end of claw 8
8. PE with a broad band of canaliculi arising from the anterolateral areola on the PE and reaching to about the innermost seta; posterior to leg IV insertion with several groups of canaliculi. *C. emblematus* sp. nov.
 PE with canaliculi near the innermost seta but not in form of a band that reaches the anterolateral areola; posterior to leg IV without canaliculi. *C. adonis* sp. nov.

ACKNOWLEDGEMENTS

I thank the Australian Biological Resources Study for funding, the Australian Institute of Marine Science for providing infrastructure support, the Great Barrier Reef Marine Park Authority for permission to collect mites in the Marine Park, and Mark Judson, Ilse Bartsch and Gordon Nishida for loan of specimens. I also acknowledge Carolina Bastidas, John Benzie, Guillermo Diaz-Pulido, Katharina Fabricius, Doug Fenner, Angus Thompson, Sven Uthicke

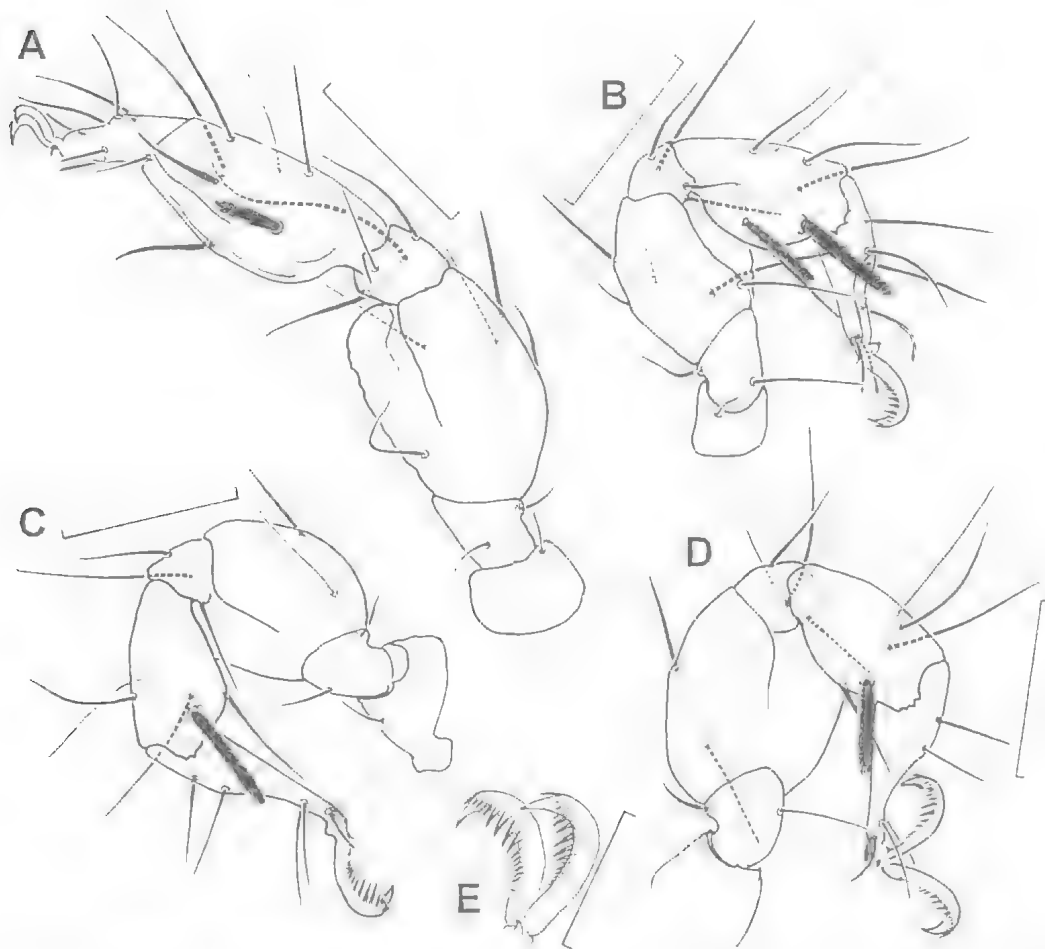


FIG. 12. *Copidognathus prideauxae* sp. nov., ♂; A, leg I, medial view; B, leg II, medial view; C, leg III, medial view; D, leg IV, medial view; E, detail of claws on tarsus II, ventral view. Scale bars: A-D = 50µm; E = 25µm.

and Irena Zagaroskis for collecting some of the material.

LITERATURE CITED

- BARTSCH, I. 1981. Halacaridae (Acari) aus dem Kanal von Moçambique. *Cahiers de Biologie Marine* 22: 35-63.
1989. New species of *Copidognathus* (Acari: Halacaridae) from Hawaiian Islands. *Bishop Museum Occasional Papers* 29: 138-148.
1992. Halacaridae (Acari) from Hong Kong. Three new species of *Copidognathus*. *Entomologische Mitteilungen aus dem zoologischen Museum Hamburg* 10: 229-241.
1997. Copidognathinae (Halacaridae, Acari) from northern Australia; description of four new species. Pp. 231-243. In Hanley, J.R., Caswell, G., Megirian, D., & Larson, H.K. (eds) *Proceedings of the Sixth International Marine Biological Workshop. The marine flora and fauna of Darwin Harbour, Northern Territory, Australia.* (Museums and Art Galleries of the Northern Territory & Australian Marine Sciences Association: Darwin).
- NEWELL, I.M. 1947. A systematic and ecological study of the Halacaridae of eastern North America. *Bulletin of the Bingham Oceanographic Collection* 10: 1-232.
1984. Antarctic Halacaroida. *Antarctic Research Series* 40: 1-284.
- OTTO, J.C. 2000a. Halacaridae from the Great Barrier Reef and Coral Sea: the genera *Lohmannella*, *Scaptognathides* and *Scaptognathus* (Acarina: Halacaridae: Lohmannellinae). *Memoirs of the Queensland Museum* 45: 535-555.
- 2000b. *Acarochelopodia* and *Actacarus* species (Acari: Halacaridae) from Australia, with remarks on *A. pacificus* and *A. orthotectus*. *Species Diversity* 5: 111-127.



A NEW SPECIES OF TORRENT-DWELLING FROG (ANURA: HYLIDAE: *LITORIA*)
FROM THE MOUNTAINS OF INDONESIAN NEW GUINEA (WEST PAPUA)

STEPHEN J. RICHARDS

Richards, S.J. 2001 06 30: A new species of torrent-dwelling frog (Anura: Hylidae: *Litoria*) from the mountains of Indonesian New Guinea (West Papua). *Memoirs of the Queensland Museum* 46(2): 733-739. Brisbane. ISSN 0079-8835.

Litoria macki sp. nov. from the mountains of West Papua, Indonesia, is a torrent-dwelling species characterised by medium size (adult ♂ 42.1-45.7mm SVL), unwebbed fingers, and prominent conical tubercles on the dorsum and limbs. The new species most closely resembles *L. spinifera* (Tyler), from which it can be distinguished by its larger size and different advertisement call. The calls of *L. macki* and *L. spinifera* are described and compared, and natural history observations on *L. spinifera* are presented. □ *Torrent-dwelling frog, West Papua, new species.*

Stephen Richards, School of Tropical Biology, James Cook University, Townsville 4811 (present address, Vertebrate Department, South Australian Museum, North Terrace, Adelaide 5000); 11 August 2000.

Torrent-dwelling hylid frogs within *Litoria* are a diverse assemblage reaching their greatest diversity in the mountains of New Guinea. All species for which life history features are documented lay unpigmented, macrolecithal eggs and have tadpoles with dorsoventrally flattened bodies and large, ventral suctorial mouthparts (Haas & Richards, 1998; Tyler & Davies, 1978). The *L. becki* species-group (Tyler & Davies, 1978) contains 5 predominantly montane torrent-dwelling frogs (*L. becki*, *L. micromembrana*, *L. modica*, *L. pratti* and *L. spinifera*) from mountains of New Guinea. These species are most easily distinguished from other torrent-dwelling *Litoria* by their medium size (♂♂ and ♀♀ to about 42mm and 53mm, respectively) and long, unwebbed fingers (Tyler & Davies, 1978).

Litoria spinifera (Tyler, 1968) is distinctive within the *L. becki* group with a sharply pointed snout and greatly enlarged tubercles on the dorsum, eyelids, tarsus and foot (Tyler, 1968). It was described from a large series of frogs collected by Mr Fred Parker at altitudes of 1000 - 1500m in dense rainforest S of Kundiawa in the central mountains of PNG (Tyler, 1968). The type series was collected 'in the vicinity of small waterways', where they were found among leaves near the streams during the day and on leaves overhanging the water at night (Tyler, 1968). Nothing else is known about its biology. During 1997 and 1998, I recorded its advertisement call and made observations on its general natural history in the Crater Mountain Wildlife Management Area (CMWMA), in Eastern Highlands Province, PNG.

Conservation International's 1998 biodiversity survey of the rugged Wapoga River headwaters region of West Papua (Mack & Alonso, 2000) accumulated a significant collection of torrent-dwelling hylid frogs (Richards, S.J., Iskandar, D. & Allison, A. in Mack & Alonso, 2000:54-57). Among these is an undescribed *Litoria* that resembles *L. spinifera* in its possession of large conical tubercles on the dorsum and limbs, but differs from that species in its larger size and different advertisement call.

In this paper I describe the new species from West Papua, and analyse and compare its vocalisations with those of *L. spinifera*. I also present brief observations on the natural history of *L. spinifera* in the CMWMA.

MATERIALS AND METHODS

Specimens are deposited in the Museum Zoologie Bogor (MZB), Indonesia, the Queensland Museum (QM), Australia, and the South Australian Museum (SAMA), Australia. Measurements (to the nearest 0.1mm) were taken with dial callipers and a stereomicroscope fitted with an ocular micrometer, and follow Menzies (1993). They are: SVL (snout-vent length), TL (tibia length), HW (head width at tympanum), HL (head length from tip of snout to posterior edge of tympanum), EYE (horizontal eye diameter), TYM (horizontal tympanum diameter), IN (inter-narial distance), EN (distance between anterior edge of eye and posterior edge of naris), 3FD (width of 3rd finger disc at right angle to digital axis) and 3FP (width of penultimate

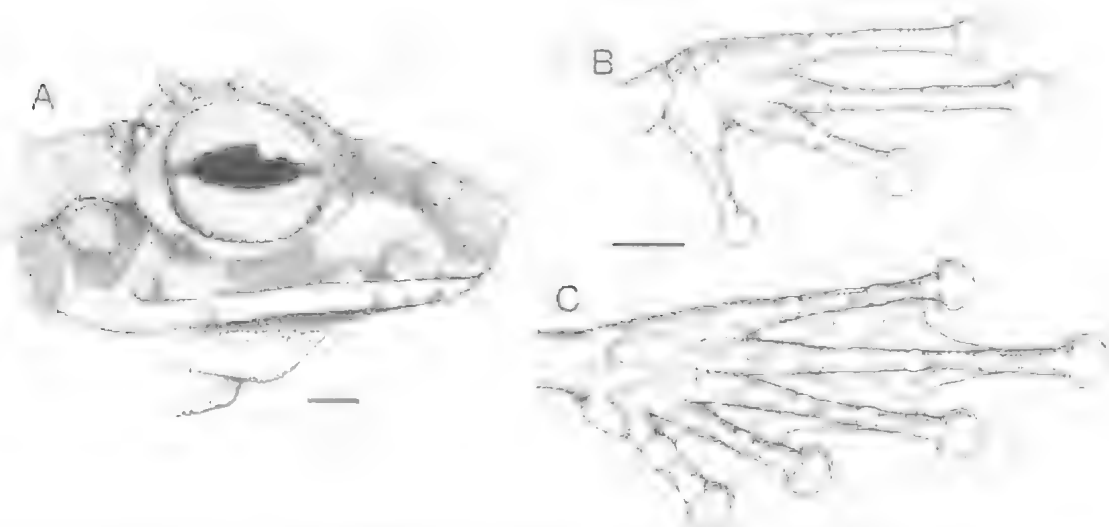


FIG. 1. *Litoria macki* sp. nov. (QMJ75810). A, lateral view of head; B, palmar view of hand; C, plantar view of foot. Scale bars = 2mm.

phalanx of 3rd finger), 4TD and 4TP (4th toe disc and 4th toe phalanx, as for 3rd finger).

Calls were recorded with a Sony Professional Walkman tape recorder and Sony SMZ-200 microphone, and were analysed with the sound analysis program Avisoft SAS-Lab Pro. Note structure was highly variable, both within and between call sequences and individual males. Variation involved the degree of pulse definition, and the presence or absence of minor pulses in terminal portions of the note. In an attempt to attain consistency only well defined pulses and pulses that contributed substantial energy to the note, were calculated for comparisons among species.

SYSTEMATICS

Litoria macki sp. nov. (Figs 1-6)

ETYMOLOGY. Named for Dr Andy Mack in appreciation of his unfailing encouragement and support and in recognition of his passion for conservation and science education in New Guinea.

MATERIAL. HOLOTYPE: MZB Amp.3870, adult ♀, collected by S.J. Richards and M. Moore, Wapoga Alpha mineral exploration camp, West Papua, Indonesia, 3°08.687'S, 136°34.423'E, 1070m, 17.iv.98. PARATYPES: MZB Amp.3871, 3872, QM J75810, SAMA R55363 same collection data as holotype, SAMA R55364 collected by M. Moore at Lagori Landing Site 21 (LS-21), West Papua, Indonesia, 3°00.348'S, 136°33.412'E, 275m, 26. iv.98.

DIAGNOSIS. A medium-sized *Litoria*, ♂♂ 42.1-45.7mm SVL, distinguished from all known

New Guinea species except *L. spinifera* by the combination of: 1, blotched green and brown dorsally in life; 2, canthus rostralis well-defined, moderately curved; 3, fingers long, unwebbed; 4, large conical tubercles on tarsus and foot, and on dorsum (concentrated on head and eyelids). Distinguished from *L. spinifera* by its larger size (SVL of male *L. spinifera* 35.3-42.3) and different advertisement call, which consists of a rapidly-repeated series of loud, bell-like notes in which note repetition rate, note length, and pulses/note increase during the call sequence.

DESCRIPTION OF HOLOTYPE. An adult ♂ measuring: SVL 45.7; TL 29.0; HW 15.6; HL 16; EYE 5.5; EN 4.0; IN 5.1; TYM 2.0; 3rd finger 1.2; 3rd disc 2.9; 4th toe 1.2; 4th disc 2.5. Body slender, limbs long (TL/SVL 0.634). Head slightly longer than broad (HL/HW 1.04), more than one third of snout-vent length (HL/SVL 0.35); snout slightly pointed in dorsal view, pointed in lateral view, projecting slightly beyond lower jaw. Canthus rostralis well-defined, moderately curved, loreal region strongly concave. Nostrils close to tip of snout, intermarial distance greater than distance between snout and naris (EN/IN 0.784). Eyes large, prominent (EYE/SVL 0.12), pupil horizontal, eyelid without reticulations. Vomerine teeth in two prominent oblique ridges between the choanae, vocal slits present. Tongue cordiform. Tympanum clearly visible, but dorsal edge obscured by prominent, slightly curved supratympanic fold. Fingers long, unwebbed,

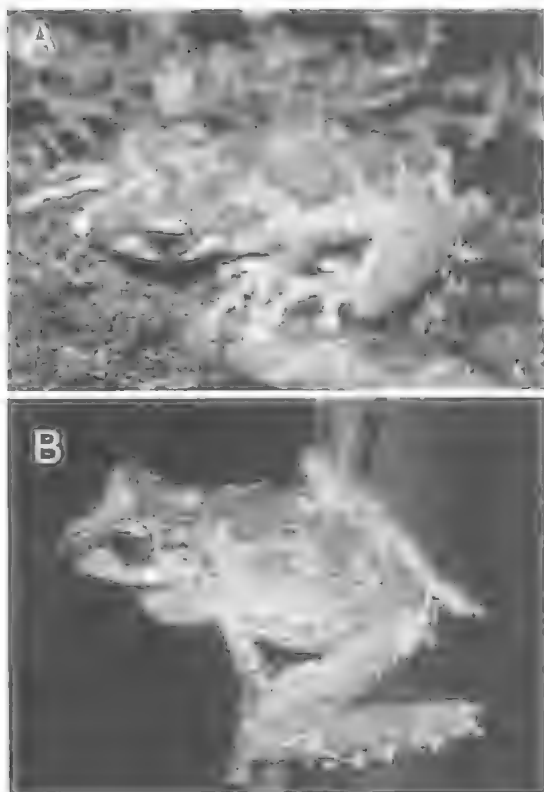


FIG. 2. A, adult *Litoria macki* sp. nov. from Wapoga River headwaters, West Papua. B, adult *L. spinifera* from Maimafu, Eastern Highlands Province, PNG.

relative lengths $3 > 4 > 2 > 1$, terminal discs large (3FP/3FD 0.41); A brown nuptial rugosity on first finger extends distally to level of penultimate tubercle. Toes 2/3 webbed, web reaching to just below penultimate tubercle on 4th toe, and nearly to disc on toes 2, 3 and 5. relative lengths $4 > 5 = 3 > 2 > 1$, terminal discs large (4TP/4TD 0.48). Conical tubercles on limbs (including heel) and dorsum, concentrated on head and eyelids, and on outer edge of tarsus and foot.

In life, mottled with large patches of brown and green dorsally, including dorsal surfaces of legs. Yellow in groin and axilla. Laterally pale yellow grading to white anteriorly and ventrally. Venter white, mottled with faint brown pigmentation. Iris gold with purple reticulations. Tubercles beneath vent white. In preservative brown dorsally, with extensive blue (green in life) patches. Pale yellow lateral and inguinal regions have faded to white.

VARIATION. The paratypes are adult males (SVL 42.1–45.3) and the colour pattern is uniform in the type series: in life all were blotched with brown and green dorsally. The size and distribution of tubercles on the dorsum and legs are variable but in all specimens tubercles on the eyelids, tarsus and heel are prominent. Measurements are summarised and compared with *C. spinifera* in Table 1.

ADVERTISEMENT CALL. The advertisement call is a series of 14–44 bell-like notes lasting about 7–50 seconds. Dominant frequency is 2606–3144Hz. A consistent and distinctive feature of the call is an increase in note repetition rate and pulses/note in terminal sequences (Fig. 5; Table 2). Individual notes are about 0.02s in length at the beginning of a call sequence and contain a single pulse. During the call sequence note length increases to 0.04–0.06s and the number of pulses/note increases to 6–8. A call sequence is illustrated in Fig. 5 and structural features are summarised in Table 2.



FIG. 3. Torrential stream habitat of *L. macki* in lower montane rainforest, West Papua.

TABLE 1. Morphological comparison of ♂ types of *Litoria macki* sp. nov. and ♂ *L. spinifera* (Tyler). Measurements involving finger and toe discs only recorded where discs are well-preserved.

	<i>Litoria macki</i> (n = 6)		<i>Litoria spinifera</i> (n = 8) CMWMA (see text)		<i>Litoria spinifera</i> (n = 12) from vicinity of type locality	
	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range
SVL	43.93 (1.36)	42.1-45.7	38.98 (1.42)	37.4-41.4	37.26 (1.29)	35.3-39.4
TL/SVL	0.629 (0.016)	0.604-0.650	0.632 (0.017)	0.609-0.658	0.657 (0.020)	0.630-0.691
EYE/SVL	0.125 (0.009)	0.114-0.142	0.130 (0.003)	0.126-0.135	0.116 (0.009)	0.107-0.137
EN/IN	0.664 (0.075)	0.592-0.784	0.630 (0.032)	0.592-0.680	0.698 (0.052)	0.615-0.829
HW/SVL	0.340 (0.005)	0.335-0.349	0.348 (0.005)	0.341-0.355	0.352 (0.010)	0.337-0.371
3FP/3FD	0.402 (0.029)	0.370-0.448	0.456 (0.036)	0.416-0.500	0.449 (0.022)	0.409-0.476
4TP/4TD	0.503 (0.015)	0.480-0.520	0.567 (0.058)	0.523-0.666	0.512 (0.032)	0.473-0.588
3FD/SVL	0.064 (0.004)	0.061-0.073	0.057 (0.002)	0.053-0.059	0.058 (0.002)	0.053-0.061
4TD/SVL	0.055 (0.005)	0.050-0.064	0.051 (0.002)	0.048-0.054	0.050 (0.003)	0.047-0.059

NATURAL HISTORY. Males called at night from small trees adjacent to and hanging over small (<5m wide) torrential streams in closed-canopy rainforest (Fig. 3). They were never observed in swampy or slow-flowing aquatic habitats. Perch sites were high above or adjacent to the water, normally exceeding 2m high, but two frogs were observed on perches about 1m above the water. Several species of suctorial tadpoles were observed in streams occupied by this species, but it is not possible to associate any of these with the new species.

DISTRIBUTION. Known only from 2 localities in the mountainous headwaters region of the Wapoga River in NW West Papua, Indonesian New Guinea (Fig. 4).

COMPARISON WITH OTHER SPECIES AND DISCUSSION. Lack of webbing between the fingers and presence of prominent conical tubercles on the dorsum and limbs will distinguish *L. macki* from all New Guinea *Litoria* except *L. spinifera*. I have examined 7 paratypes (SAMA R6295-6301) and 5 additional specimens (SAMA R9167, SAMA R9108A-D) of *Litoria spinifera* collected in the vicinity of the type locality, and compared them with 8 specimens (SAMA R55357-62; UPNG 9963-4) from the Crater Mountain Wildlife Management Area (55-75km SE of Kundiawa). The frogs from CMWMA have prominent tubercles along the edge of the tarsus and foot (Fig. 2) and agree in all other respects except minimum adult size with the type series (Table 1). The minimum SVL reported for the type series is 38.4mm (Tyler 1968) but the minimum for frogs from CMWMA is 36.7mm. However re-measurement of the seven *L. spinifera* paratypes shows that six

specimens have an SVL less than 38.4mm and the minimum SVL of this sample is 35.5mm. The smallest adult male *L. spinifera* that I have examined has an SVL of 35.3mm and the mean SVL of frogs from the vicinity of the type locality and from CMWMA are 37.26 and 38.98mm respectively (Table 1). There is therefore complete overlap between the type series and specimens from the CMWMA in all characters examined and I have no hesitation in referring the CMWMA specimens to this species.

In contrast there is no overlap in size between the type series of *L. macki* and the eight *L. spinifera* from the CMWMA (SVL 42.1-45.3 vs 36.7-41.4 in *spinifera*; Table 1), and only marginal overlap between *L. macki* and the large type series of *L. spinifera* (29 males from Oruge and vicinity measuring 35.5-42.3mm; upper size limit based on Tyler, 1968) (Table 1). Size of finger discs is another character that is useful for distinguishing between these two species. The disc of the third finger is larger in proportion to SVL in *L. macki* than in *L. spinifera* (3FD/SVL 0.061-0.073 vs 0.053-0.061; Table 1). Only one of the *L. spinifera* examined had a 3FD/SVL ratio that was as large as the smallest ratio recorded for *L. macki*.

Difference in size alone would be insufficient to warrant recognition of the Wapoga specimens and *L. spinifera* as distinct taxa, given that the populations are allopatric and separated by nearly 1000km (Fig. 4). However *L. macki* can be further distinguished from *L. spinifera* by its advertisement call, which is a short sequence of 14-44 explosive notes (see above). In contrast the calls of *L. spinifera* are distinctly pulsed musical notes uttered singly at regular or irregular intervals of 1.5-8 seconds (Fig. 5). The call of *L.*

TABLE 2. Advertisement call characteristics of *Litoria macki* sp. nov. and *L. spinifera* (Tyler). ¹ structural features of notes based on two call series only, ² only a short portion of a much longer sequence was recorded, ³ excluding territorial calls. Data are presented as mean (SD) range.

	<i>Litoria macki</i>		<i>Litoria spinifera</i>	
Frog number (call sequences)	QM J75810 (n = 3) ¹	SAMA R 55363 (n = 3)	Herowana SAMA R55361 (n = 1) ²	Maimafu SAMA R55357 (n = 2)
Date	17.iv.98	17.iv.98	3.xii.98	1.xii.97
Snout-vent length (mm)	42.1	43.7	41.4	39.5
Temperature °C	20.8	22.5	20.6	20
Full call sequence				
Total notes in sequence	18-44	14-19	6	25-49
Call duration (s)	10.3-48.7	7.2-15.4	22.75	97.2-125.3
Note repetition rate (notes/s)	0.9-1.66	1.22-1.82	0.22	0.25-0.39
Note duration (s) ³	0.04 (0.01) 0.015-0.084	0.03 (0.01) 0.015-0.066	0.025 (0.009) 0.019-0.045	0.03 (0.01) 0.013-0.095
Pulses per note ³	3.2 (2.4) 1-9	3.0 (2.0) 1-8	3.5 (1.22) 3-6	4.04 (1.5) 2-9
Single-pulse notes?	Yes	Yes	No	No
Dominant frequency (Hz)	2606-2842	2961-3144	2885-3015	1335-2821
Introductory notes				
Note repetition rate (notes/s)	0.78-1.16	0.84-0.92	-	-
Terminal notes				
Note repetition rate (notes/s)	1.9-2.39	2.56-2.57	-	-
Territorial calls				
Type 1 (n = 6) Length (s)	-	-	-	0.358 (0.09) 0.21-0.44
Number of pulses	-	-	-	34.83 (9.5) 19-44
Type 2 (n = 4) Number of notes per sequence	-	-	-	5-6
Note repetition rate (notes/s)	-	-	-	2.24 (0.32) 2.0-2.7

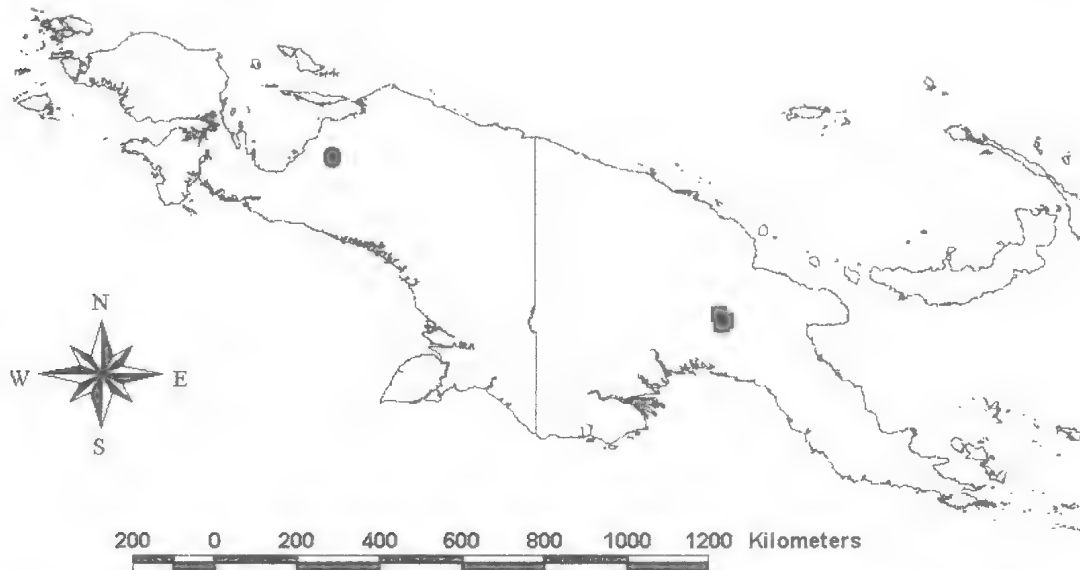


FIG. 4. Distribution of *L. macki* (●) and *L. spinifera* (■: Crater Mountain sites only) specimens examined during this study.

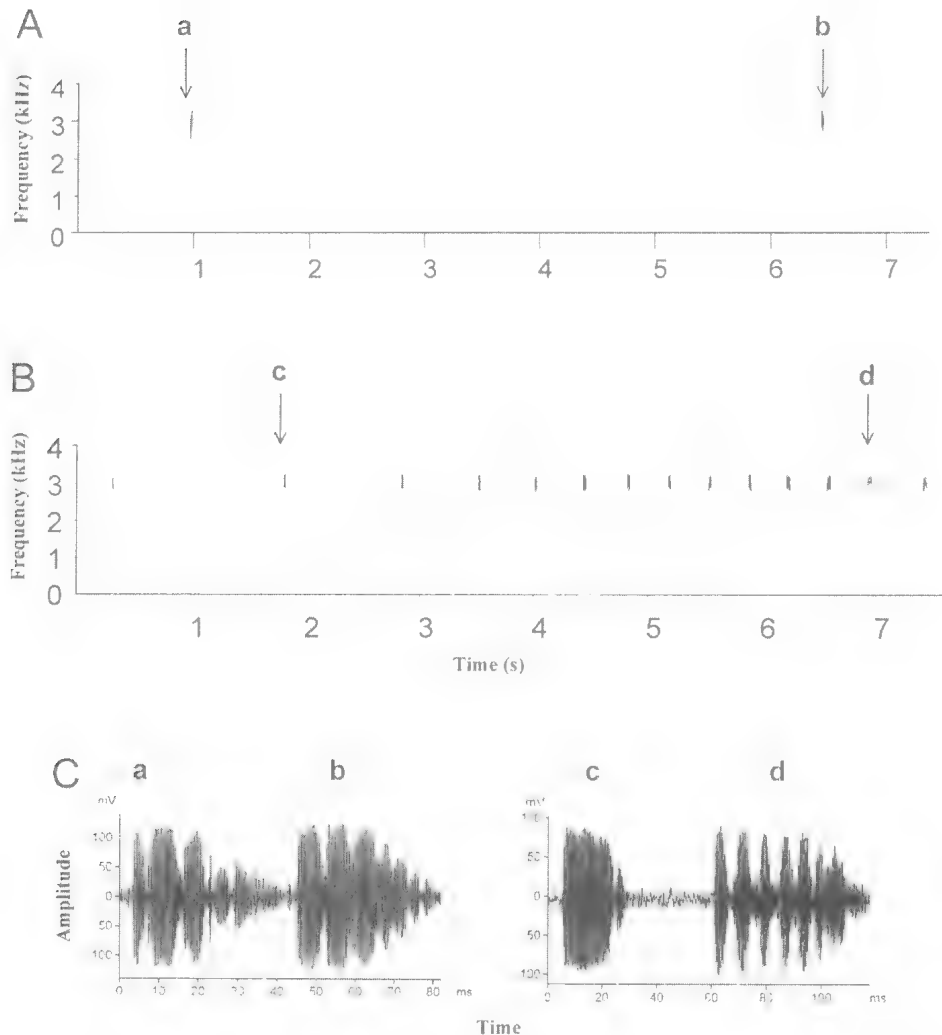


FIG. 5. Advertisement calls of A, *Litoria spinifera* (SAMA R55361) from Herowana, PNG, two consecutive notes from a long series at an air temperature of 20.6°C; B, *Litoria macki* (SAMA R55363) at an air temperature of 22.5°C, audiospectrogram of full call sequence showing increasing note repetition rate during call sequence; C, wave forms of notes indicated, showing distinctly pulsed calls of *L. spinifera* and change in pulse number during call sequence of *L. macki*.

spinifera also differs from that of *L. macki* in the following features: in *L. spinifera* all notes are distinctly pulsed (vs single-pulse introductory notes in *L. macki*; Table 2), note repetition rate is much slower than that of *L. macki* at similar temperatures, and note repetition rate and pulses/note do not increase dramatically during a sequence of calls. The call of *L. spinifera* is described in more detail below and structural features are presented and compared with *L. macki* in Table 2.

DISTRIBUTION AND NATURAL HISTORY OF *LITORIA SPINIFERA*

Litoria spinifera was previously known from several localities SW of Gumine in Chimbu Province. Although precise coordinates are not available, all of these sites are clustered in an area extending from approximately 6°12'S, 144°57'E in the north to approximately 6°43'S, 144°43'E in the south. *L. spinifera* was a common species in the Crater Mountain Wildlife Management Area (Herowana 6°39'14.5"S, 145°11'49.8"E; Maimafu 6°30'06.0"S, 145°01'59.1"E) during

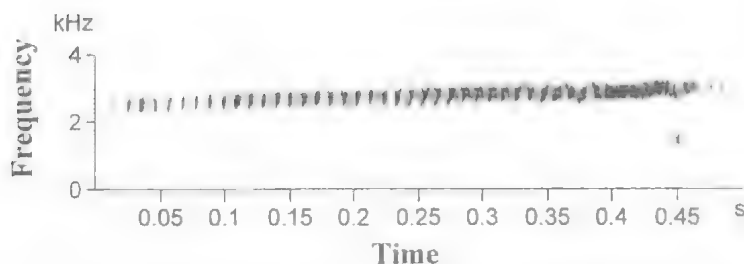


FIG. 6. 'Territorial' call of *Litoria spinifera* from Maimafu, given during vocal interaction with another calling frog.

November-December 1997 and 1998, and in January 2000 adults were heard calling, and several immature specimens were observed, at the Wara Sera Research Station (6°43.423'S, 145°05.693'E) (Fig. 4). The CMWMA records extend the known distribution of this species about 40km to the east.

At Herowana and Maimafu males called from leaves one to 3 metres above the ground, above or adjacent to small torrential streams. At Herowana males were common along streams running through disturbed rainforest and old gardens, suggesting that this species is tolerant of significant human disturbance. Some of these streams had beds that were heavily silted due to erosion from the surrounding denuded hill slopes.

ADVERTISEMENT CALL OF *LITORIA SPINIFERA*. The advertisement call of *L. spinifera* is a single distinctly pulsed note. Each note consists of 2-9 pulses (Fig. 6; Table 2), and notes are repeated at intervals of about 1.5-8 seconds for very long periods. Two complete call sequences recorded at Maimafu lasted for 97.2 seconds and 125.3 seconds (Table 2). Two other call-types, tentatively identified as territorial calls, were heard but were much less common and only produced by one male in response to calls of a nearby conspecific. Territorial call type 1 consisted of a single drawn out note with substantially more pulses than 'normal' calls (Table 2). Territorial call type 2 involved the production of 5-6 notes in rapid succession, with a repetition rate substantially higher than that of the whole call sequence (Table 2). Both of these territorial call types were uttered intermittently during long sequences of 'normal' (advertisement) calls.

All calls are finely tuned, with energy concentrated in narrow bands giving them a musical quality. In calls from Herowana, energy

is concentrated in a single band, but in calls from Maimafu energy is concentrated in 2 distinct, harmonically related bands. In some notes the lower frequency is dominant; in others the higher frequency dominates.

ACKNOWLEDGEMENTS

I am extremely grateful to Dr Arie Budiman of Puslitbang Zoology, and the head of Museum Zoologicum Bogoriense - LIPI, Ibu Liliek Prijono, for their assistance in Jakarta and Bogor. Dr Djoko Iskandar assisted in many ways in the field, and I am most grateful for his input to this project. This research was part of Conservation International's Rapid Assessment Program, and I greatly appreciate their assistance. Funding support was provided by the CI-USAID Cooperative Agreement # PCE-5554-A-00-4028-00. I am especially grateful to Andy Mack, Yatna Supriatna, and Burke Burnett of CI for support during the survey, and to Mike Moore who helped collect. P.T. Freeport Indonesia provided logistical support for which I am most grateful. Mike Tyler commented on the manuscript and Bronwen Scott produced Fig. 1. Andy Mack helped produce the map.

LITERATURE CITED

- HAAS, A. & RICHARDS, S.J. 1998. The correlation of cranial morphology, ecology and evolution in suctorial tadpoles of the Australian genera *Litoria* and *Nyctimystes* (Amphibia: Anura: Hylidae: Pelodyadinae) *Journal of Morphology* 238: 109-141.
- MACK, A. & ALONSO, L. (eds) 2000. A biological assessment of the Wapoga river area of northwestern Irian Jaya, Indonesia. RAP Bulletin of Biological Assessment 14. (Conservation International: Washington).
- MENZIES, J.I. 1993. Systematics of *Litoria iris* (Anura: Hylidae) and its allies in New Guinea and a note on sexual dimorphism in the group. *Australian Journal of Zoology* 41: 225-255.
- TYLER, M.J. 1968. Papuan hylid frogs of the genus *Hyla*. *Zoologische Verhandlungen* 96: 1-203.
- TYLER, M.J. & DAVIES, M. 1978. Species-groups within the Australopapuan hylid frog genus *Litoria* Tschudi. *Australian Journal of Zoology* (supplement 63): 1-47.



THE HELICINID LAND SNAIL *PLEUROPOMA EXTINCTA* (ODHNER, 1917) AS AN ENVIRONMENTAL INDICATOR IN ARCHAEOLOGY

CASSANDRA ROWE, JOHN STANISIC, BRUNO DAVID AND HARRY LOURANDOS

Rowe, C., Stanisic, J., David, B. & Lourandos, H. 2001 06 30: The helicimid land snail *Pleuropoma extincta* (Odhner, 1917) as an environmental indicator in archaeology. *Memoirs of the Queensland Museum* 46(2): 741-770, Brisbane. ISSN 0079-8835.

Land snails have long been used as palaeoenvironmental indicators in some parts of the world, but in Australia they have received little attention. Here we present new data on the geographical distribution and ecological characteristics of the helicimid *Pleuropoma extincta* (Odhner, 1917). The species is confined to the limestone outcrops of the Chillagoe Formation where it occurs abundantly both as living populations on the limestone rock and associated vegetation, and as dead shells in the litter deposits. After analysing >1,100 modern snail shells from 24 collection localities (from two major limestone regions within the formation), we argue that the sensitivity of shell growth (measured as size-correlated differences in whorl counts) to environmental moisture variation in *P. extincta* makes this species particularly suitable for palaeoenvironmental research. Differences in whorl counts of sub-fossil *P. extincta* shells from archaeological excavations at Hay Cave, in tropical northeastern Australia, are then investigated. We conclude with observations about the implications of the land snail shell sequence for the nature and timing of changes in rainfall levels during the last 19,000 years in north Queensland, and how these changes compare and contrast with existing palynological trends for the Atherton Tableland nearby. □ *Land snails, Helicinidae, Pleuropoma extincta, palaeoenvironments, archaeology, north Queensland, Australia.*

Cassandra Rowe and Bruno David (e-mail: bruno.david@arts.monash.edu.au), Department of Geography & Environmental Science, Monash University, Wellington Road, Clayton 3800; John Stanisic, Queensland Museum, PO Box 3300, South Brisbane 4101; Harry Lourandos, Department of Anthropology & Sociology, University of Queensland, St Lucia 4072, Australia; 10 November 2000.

In Australia, the use of archaeologically obtained land snails for palaeoenvironmental reconstructions is in its infancy. This is despite their frequent presence in excavated sites. Some of the problems associated with the utility of land snails in archaeological analysis were outlined by Evans (1972) and highlighted by other authors since, especially in Europe (e.g. Carter, 1990; Connah & McMillan, 1964; Sparks, 1969). Difficulties arise in two major areas: the level of knowledge about the land snail species to be used, including not only their taxonomic status but also their behavioural and ecologic traits; and the taphonomic status of the excavated samples. These difficulties are equally, if not more, applicable in the Australian sphere. This paper presents new data from north Queensland, addressing these issues so as to investigate late Quaternary palaeoenvironments along the western slopes of the Great Dividing Range, an area hitherto poorly researched.

QUATERNARY LAND SNAILS: HISTORY OF RESEARCH

Study of gastropod molluscs from Pleistocene archaeological deposits began in the 19th century, and the possibility of using snails as indicators of past climates, local environments and as chronological indicators has been recognised since at least this time (Kennard, 1897; Lowe & Walker, 1984). As in other branches of palaeontology, much of the early work was concerned with taxonomy; relatively little attention was paid to palaeoecological considerations. By the late 19th and early 20th centuries, however, researchers in the United Kingdom began to use molluscs as palaeoclimatic indicators and as a means of dating geological events (Kennard, 1897; Woodward, 1908). During 1919 to 1939, numerous investigations followed their lead. These studies were usually published as appendices to archaeological reports. One of the earliest studies concerned the Neolithic (4,000-2,400 BC) flint mines of Grimes Graves in Norfolk, where land snails were used not only as indicators of past

landscapes, but also as evidence for the post-glacial antiquity of the mines — at that time an issue in considerable dispute (Evans, 1972).

Despite such promising pioneering works emanating from the UK (and to some degree from central Europe, particularly Czechoslovakia), to this day the analysis of land snails from archaeological deposits continues to be largely ignored in many parts of the world. Yet the argument for using land snails in palaeo-ecological reconstructions seems irresistible. Alternations of cool and warm periods, spanning various lengths of time from decades to thousands of years, are represented by soil horizons which, when not decalcified, usually contain molluscs of various species. Such changing climatic conditions during the Quaternary have been successfully identified by land snail analysis in Czechoslovakia, in much the same way that pollen has been used to define various interglacial periods. Not only can the distinction between interglacial, interstadial and glacial stages be recognised via land snails, but in many cases the fauna are sufficiently diagnostic to make relatively fine-grained climatic determinations for some periods of time (cf. Evans, 1972).

In a study with particular relevance to the current investigation, Solem (1972) documented land snails from deposits recovered in the Aq Kupruk Caves, Afghanistan. He used the general abundance of taxa in the land snail assemblage as well as size differences in the enid *Subzebrinus eremitus* (Benson, 1849), a pulmonate gastropod, to postulate prehistoric changes in moisture patterns. However, he readily acknowledged that his conclusions were restricted by the absence of knowledge about the ecology and distribution of the contemporary land snail fauna of the region and a lack of data on environmental variation within local species. In spite of these shortcomings Solem's (1972) analyses demonstrated the principle that changes in the shell-size of land snails could be used to determine past changes in environmental moisture levels.

Brief discussions of research in central Europe, the Middle East, Africa and North America can be found in Evans (1969) and Goodfriend (1992), and will not be recounted here. However, in central Europe and North America, land snail analysis is of considerable importance in various lines of Quaternary research. This is due in large part to their widespread occurrence in areas of calcareous loess (Evans, 1972).

LAND SNAIL RESEARCH IN THE UK: EMERGENCE OF A TECHNIQUE

In Britain, numerous regional studies have looked to land snails to investigate the timing and extent of human-induced landscape clearances from the Neolithic to the Bronze Age (Wainwright & Davies, 1995). Where land snails were once used to look at general changes in land-use patterns (e.g. Evans 1971a, 1971b for southern England), they are now being used for much higher resolution mapping of archaeological landscapes, typically at scales of about 35-80km² (e.g. Allen 1997, in press). Several factors have contributed to this. Land snails are abundant in many types of depositional contexts (including oxidised sediments); these are usually identifiable to species; and they are visible in the field, thus allowing preliminary assessments of local depositional environments (Porch, in prep.). Moreover, their appeal is also directly related to a fundamental limitation of pollen research in the UK, where an absence of peat and linnic deposits from the large tracts of chalk and limestone in southern, central and eastern England renders pollen analysis inappropriate (Evans, 1972). Pollen analysis until recently has been able to reveal virtually nothing about the environmental and ecological history of the chalklands (but see for example Seafie, 1995; Sharples, 1991). This is particularly unfortunate given the importance of such environmental settings to settlement and agriculture during prehistoric and Roman times (Evans, 1972). In contrast, palaeoenvironmental research based on land snails has enabled conclusions to be drawn on the nature of people-land relations for various periods in prehistory, including the timing of landscape clearances, the onset of agricultural practices, and the emergence of intensified settlement systems (Evans, 1972). The thrust of Evans' own work shows that ecological information can be gained from land snails with which patterns of land-use change can be addressed. Given these research foci, it is common to find in the archaeological literature discussions of land snails and the presentation of data included under captions such as "Evidence for the environment and farming economy". This is particularly so when sites such as barrows (burial mounds), pits, hillforts, pastureland and ploughzones are considered (Allen, 1995a).

It has also been recognised for some time, largely from the results of pollen analysis, that

many parts of Britain which are today open country were once forested. The East Anglian Breakland and the North York Moors are classic examples, the former having been cleared by Neolithic people some 3,000 BC, the latter during the Bronze Age by around 1,550 BC (Evans, 1972). In view of this, it has generally been assumed that the chalk and limestone upland regions were likewise once forested, having suffered a similar history of forest clearance through the actions of prehistoric farmers. By undertaking land snail analysis, landscape clearance dating as far back as the 4th millennium BC has been confirmed. As a result, it is now thought that few, if any, parts of the British Isles can today be thought of as entirely natural (Evans, 1972).

The Buckskin Barrow site at Basingstoke, Hampshire, provides a good example of how changing frequencies of molluscan faunas with distinctive ecological affiliation can be used to identify changes in patterns and intensities of land use. An excavated section through a series of silts and mixed deposits suggested the clearance of deciduous woodlands during the Late Neolithic to Early Bronze Age. This clearance was associated with pre-barrow features and a cremation pit. Subsequently, short-grazed grasslands became established during the Middle to Late Bronze Age. By the Iron Age, the site had become overgrown by long grasses and shrubs (indicating very little or low pressure land-use) followed by intermittent arable and pastoral activity, resulting in erosion of the barrow monument (Allen et al., 1995). Consequently, molluscan evidence indicated to the excavators that major changes had taken place in systems of land use at Basingstoke since the late Neolithic, and that these changes could be divided into a number of well-defined demographic, settlement and economic systems.

LAND SNAIL ANALYSIS IN AUSTRALIAN ARCHAEOLOGY

Australian archaeological site reports typically include site descriptions, vertebrate faunal lists and a detailed evaluation of stone artefacts, while rarely making even a passing note of land snails. They are rarely identified even when their presence is noted, and are rarely incorporated in ensuing discussions (David & Stanisic, 1991). To illustrate this point: in SE Australia, almost all non-marine molluscan analyses have been qualitative and peripheral to the main objectives which are generally geomorphological or

palynological in emphasis (Porch, in prep.). This is somewhat surprising given the attention often paid to palaeoenvironmental indicators such as pollen from archaeological sites. It is doubly so given the high profile of land snail research in archaeology in the UK, where most of Australia's first generation of professional archaeologists were trained in the 1960s.

BIOGEOGRAPHY OF AUSTRALIAN LAND SNAILS AND THEIR SUITABILITY AS PALAEOENVIRONMENTAL INDICATORS.

A key biological feature of terrestrial molluscs that makes them useful in climatic reconstruction is their sensitivity to environmental moisture regimes. They have not evolved totally effective structural means to prevent water loss and desiccation is their greatest enemy. This characteristic makes them especially relevant for such studies in Australia where climatic drying (with shorter intermittent wet periods) since the Miocene has been an overriding force in determining the distribution of the biota. Such climatic changes were particularly prevalent in the Quaternary when they occurred in greater rapidity (Galloway & Kemp, 1981; Kemp, 1981; Nix & Kalma, 1972).

Biogeographic analyses of Australian land snails (Bishop, 1981; Stanisic, 1994a; Solem, 1992a, b; Pokryszko, 1996) stress the post-Miocene drying of the continent as a basic factor in the evolutionary processes that have led to contemporary distribution patterns. Reasons for this have a broader ecological basis than purely snails 'drying out'. Moisture, to a large extent, also determines the distribution of vegetation systems (Webb & Tracey, 1981) so it is not surprising to find strong correlations between distribution of land snails and certain vegetation communities; particularly rainforests in eastern and northern Australia where the majority of land snail species occur (Solem, 1991; Stanisic et al., 1994; Stanisic, 1998). Such relationships with vegetation are evident not only at the community (=guild) level but also in the geographical distribution of individual species (Solem, 1991; Stanisic, 1997c, 1998). These trends are perhaps best illustrated by the current distribution of the Charopidae, a Gondwanan family that established a close relationship with rainforests during the late Cretaceous when mesic forests were more widely spread (Stanisic, 1990).

The ecological bond between land snails and rainforest is predicated on convergent habitat preference since ecological conditions that

favour the growth and persistence of rainforest, particularly high and stable moisture availability, and eutrophic soils, are also those favoured by terrestrial molluscs. For land snails, rainforests also provide shelter and food. In most cases, the present-day restriction of land snails to suitable patches of rainforest vegetation is absolute (Stanisic & Ingram, 1998) though in a historical sense these distribution patterns should be viewed as temporally dynamic (Stanisic, 1999).

Hence from a biogeographical perspective land snails are useful for determining the vicariant shattering and isolation of mesic habitats when conditions were dry and hostile. They are also useful indicators of historic dispersal routes that became available to a wide array of organisms when conditions were moister, and thus more favourable to the movement of wet-adapted organisms (Stanisic & Ingram, 1998). From an archaeological viewpoint, they would appear to be ideal candidates for palaeoenvironmental reconstruction.

ADVANCE AT A SNAIL'S PACE. So why have land snails been so rarely used in Australian archaeological studies? Kershaw et al. (in press) suggest that palaeoenvironmental research based on land snails in Australia to date, has been limited by inadequate ecological and systematic knowledge. The shortcomings in taxonomic knowledge seem to be borne out by preliminary analyses of land snail diversity in eastern Australia (Stanisic, 1994a). Since the late 1970s considerable descriptive work has been completed on land snails of the Kimberley region, central Australia and South Australia (see Solem, 1992a and accompanying references), but much remains to be done elsewhere. Several detailed regional surveys of land snails by Stanisic (1994a, 1997c, 1998) in eastern Australia demonstrate more fully the extent of these shortcomings. In southeastern Australia, Smith & Kershaw's (1979, 1981) checklists of Victorian and Tasmanian land snails form the basis of knowledge for this region, however, even these are not based on comprehensive survey work.

Nevertheless pioneering studies using these animals in palaeoenvironmental reconstruction have been attempted. David & Stanisic (1991) reported a Holocene (and possibly terminal Pleistocene) land snail sequence from Echidna's Rest, an archaeological site in north Queensland and interpreted variations in the relative

abundance of mesic and dry-adapted taxa in terms of changes in regional moisture regimes.

In a study of land snail remains relative to local environments for the past 35,000 years at Warreen Cave, southwest Tasmania, N. Porch & J. Allen (pers. comm.) argued the snails indicate environmental changes reflecting regional climatic change rather than exclusively local factors.

In a second Tasmanian study (N. Porch pers. comm.) a long sequence of land and freshwater molluscs from Pulbeena Swamp, northwestern Tasmania suggests that palaeoenvironmental trends based on pollen and ostracod sequences are supported by the molluscan sequence.

Notwithstanding these studies, the limited use of land snails in Australian archaeology is regrettable when it is realised that in many parts of Australia, other palaeoenvironmental data do not appear suited to addressing archaeological questions. Many palaeoenvironmental records are founded on pollen sequences obtained from places tens or even hundreds of km from archaeological sites.

OTHER CONSIDERATIONS. There are two major differences between the UK and Australia in this type of research. Firstly, in the UK people have been directly responsible for massive changes in vegetation communities since the Neolithic, principally through agricultural practices. Human impacts on the landscape were extreme to the point that most climate-induced changes were dwarfed by comparison. Consequently, major changes in molluscan assemblages (Allen, 1992, 1995a) can be directly attributed to human activities. This is not the case in Australia, where climate still is a major controlling force behind both vegetation and land snail changes. While anthropogenic fires in Australia could be considered to have affected environments in a similar way as human clearance in the UK, the protected nature of limestone outcrops in Australia has significantly limited the impact of fire in these environments.

Secondly, high levels of molluscan diversity in Australia over-rides abundance. This is well illustrated by the 222 Wet Tropic species known in northeastern Queensland (Stanisic et al., 1994), as against 200 for the British region as a whole. Stanisic (1994a) recorded individual southeastern Queensland sites yielding in excess of 40 species. This allows for an organisation and interpretation of species based on their environmental associations (e.g. wet vs dry

adapted [David & Stanisic, 1991; Stanisic, 1994a]) in Australia. However, given limitations in sampling methodologies as practised in Australia, where sediment samples are sieved through wire mesh of various sizes and only the fractions caught in the mesh are kept and hand sorted for land snail shells, most very small species are by-passed and therefore ignored. Procuring and processing land snail samples from sieved excavated sediments will result in the non-collection of snails smaller than the wire-mesh (David & Stanisic, 1991) which may be critical to the level of interpretation placed on analyses. As this paper aims to show, variation in shell size of particular species, no matter how small, can provide palaeoclimatic information that may over-ride issues based on biodiversity.

RESEARCH METHODOLOGIES. Two major analytical methods have been applied in palaeoenvironmental research based on fossil land snails. The first, a qualitative approach, uses a taxon's modern ecological requirements to make statements about the environment of sub-fossil assemblages (Goodfriend, 1992). In general, shells can be extracted from ancient deposits and identified to species or genus. By attributing ancient shell assemblages to their nearest present-day ecological analogues, where species composition is known to be governed by climate and local habitats, some idea of past environments can be obtained (Lowe & Walker, 1984). This methodology follows procedures outlined by Evans (1972), and has recently been characterised as standard (Cleal & Allen, 1994; Allen & Wyles, 1993).

The second, a quantitative approach, uses absolute numbers or the relative abundance of particular taxa to interpret palaeoenvironments (Goodfriend, 1992). The total number of molluscan species (living and extinct) in Britain is not more than 200, and fewer than 50 of these can generally be expected in terrestrial sites (Evans, 1972). When changing proportions of represented taxa are investigated through time, it is common to divide species into ecological categories: woodland vs. shade-loving, intermediate vs. catholic, open-country vs. closed woodland, disturbance-sensitive vs. disturbance-tolerant species (Evans, 1972; Lowe & Walker, 1984). O'Connor (1988) suggested the addition of a fifth category — wet terrestrial — after studies of molluscs as indicators of slums and ditches highlighted their benefits to the history of settlement sites in wetland areas, although Robinson (1988) is more specific in

taxonomic and ecological terms. In these contexts, the usefulness of such ecological categories to the study of past people-land relations is well illustrated by the chalkland block of Malling, Cliff and Caburn. Here, the molluscan sequence has been sub-divided into phases of mature deciduous woodland with dense leaf litter, to woodland clearance and localised ground disturbance, and finally to fluctuating pressures through a grazed, dry grassland (Allen, 1995a, 1995b).

CONCEPTS AND DIFFICULTIES. Evans (1972) noted that practical difficulties fall into two main categories: stratigraphic and ecological. In the former, variations in the horizontal and vertical distribution of land snails in soil or sediment profiles may skew death assemblages in a way not truly reflective of past populations. For example, snails may occur on rock surfaces, among trees and leaf litter, or at varying depths underground. This results in the presence of different but contemporaneous species of land snails at different vertical levels, a potential problem often accentuated by the activities of worms and other invertebrates known to significantly disturb soil profiles (David & Stanisic, 1991). At death, snails on or above the ground accumulate on the ground surface through gravity, while those buried under the ground remain *in situ*. The physical, chemical and biological soil processes acting on this signify that the 'subfossil' assemblage (including that extracted for analysis) is distinct from the 'death' assemblage, and one further stage removed from the 'living' population (Evans, 1972).

Studies from southern Britain have highlighted processes where sediment profiles have been altered, eroded or obscured to such an extent that 'stratified' data may no longer reflect real prehistoric settlement patterns (Allen, 1994). For example, the erosion of fine soil particles by sheetwash and small rills has often resulted in the regular removal of the silt, fine sand and small stone fractions of soil profiles. The effect of this in areas of soil loss has been to artificially concentrate evidence of specific types of human activity along the upper slopes. Areas of deposition tend to show a reduction in the density of such evidence on or near the ground surface, especially where total burial has taken place. Under more energetic erosion regimes, the removal, travel and physical smashing of evidence is possible (Allen, 1991, 1994).

Previous alternating, perhaps rotational farming regimes and subsequent erosional events through valley systems have been suggested as one explanation for a paucity of Neolithic and early Bronze Age settlement in Wiltshire (Evans, 1972).

Interpretations of erosion events through land snail research have been possible given that flushes of terrestrial sediments into river and/or lake systems can be identified by the presence of non-aquatic shells and sediments within a soil profile (Evans, 1972). The relative abundance of individual species of land snails within a community is partly controlled by hereditary factors congenital to those species. Some taxa, such as *Vertigo pygmaea*, are seldom abundant, irrespective of the suitability of the habitat; others, such as *Carychium tridentatum* and *Discus rotundatus*, are often prolific. Thus, ratios between species are to some extent a function of patterns of reproduction and survival (Evans, 1972). The shells of particular species of snail also vary in their ability to resist physical and chemical destruction. Hence thin-shelled taxa, such as *Oxychilus*, tend to be more readily damaged or destroyed than more robust shells, such as *Cepaea*. Some shell apices, notably those of *Pomatias elegans* and *Clausilia*, become enlarged by the accretion of calcium carbonate, and often remain in the soil for very long periods of time. The ability of some shell species to withstand both chemical and mechanical pressures during and following burial may thus cause artificial stratification down a soil profile (Evans, 1972). These issues highlight the need to include both an adequate assessment of snail behaviour and a discussion of the taphonomic status of excavated samples for each species analysed. Taking this into account, palaeoenvironmental reconstructions based on species composition or abundance in fossil assemblages depend ultimately on a knowledge of ecological factors controlling species distribution and abundance among modern land snails (Goodfriend, 1992).

ENVIRONMENTAL SETTING OF STUDY AREA

Northeastern Australia is perhaps best known for the Wet Tropics World Heritage Area, a region described as possessing great biological significance in terms of species diversity and endemism. Unlike this humid belt, however, most ecosystems in the region are seasonally stressed by drought. Their research profile,

however, does not match their geographic prominence. As Gillison (1987) noted, the distribution and ecology of vegetation surrounding the Wet Tropics World Heritage Area are poorly known. Rainforest, as defined in Australia, covers a whole range of floristically related, closed canopied communities (Webb & Tracey, 1981). These communities include not only the floristically diverse and structurally complex types requiring high rainfall, but also small patches of semi-evergreen and deciduous monsoon forests and vine thickets (Kahn & Lawrie, 1983; Winter et al., 1987).

In wet coastal areas complex mesophyll or mesophyll vine forest dominate lowlands and lower mountain slopes. Mesophyll vine forests also occur at altitudes of up to 800m on basalt soils where soil fertility is particularly favourable. However, patches of sclerophyll vegetation can occur within these rainforest massifs, generally but not exclusively where rainforest development is inhibited by poor or excessive drainage and regular disturbances (Kershaw, 1994). These vegetation patterns are replaced progressively by notophyll and microphyll vine forests, and eventually simple microphyll vine-fern thickets with increasing altitude and by notophyll vine forest with decreasing rainfall. West of the ranges there is a rapid change from rainforest to open forest as the rainfall declines sharply due to the rain-shadow effect of the mountains. This usually occurs above 600m with a transition band of tall open forest extending continuously for about 360km from Mount Halifax in the south to Mount Windsor Tableland in the north. Further west towards the Gulf of Carpentaria, eucalypt forests are drier and stunted. In this area, semi-deciduous vine thickets with relatively small and restricted distributions occur. Generally they are found in locally moist and fire shadow niches. The vine thickets that occur on the limestone outcrops of the Chillagoe Formation which encompass two major karst areas (Mitchell-Palmer and Chillagoe-Mungana) are typical.

Dry vine thickets can also occur in environments very similar to surrounding sclerophyll vegetation (Hiscock & Kershaw, 1992) and in the south, a few small patches of low, semi-deciduous, dry monsoon forest endure, scattered in an arc extending southeast from Chillagoe (Bell et al., 1987).

The Mitchell-Palmer and Chillagoe-Mungana limestones, towards the northern end of this

TABLE 1. Rainfall figures for Mitchell-Palmer (mean rainfall readings taken at Palmerville for years 1889-1998, and at Bellevue for 1957-1998).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Palmerville mean (mm)	260	259	183	49	16	12	5	4	8	19	61	158
Bellevue mean (mm)	225	207	161	30	17	8	1	6	6	15	72	156
Palmerville mean no. rain days	17	18	15	7	3	3	2	1	2	3	6	11

limestone arc, are geographically isolated from each other by the Walsh River and extend from just north of the Palmer River near Palmerville Station, to northwest of Almaden in the south (Fig. 1). In both areas the climate is basically semi-arid but highly seasonal. Vegetation on these limestone outcrops, where there is shelter from fire, is deciduous, microphyll vine thicket. Fensham (1995, 1996) denoted these vine thickets as a floristically distinct group restricted mainly to limestone karst. The relatively closed canopy of the vegetation cover and the highly dissected micro-topography of the limestone karst provide a wide range of moist, shady micro-environments favoured by land snails. Within each of the two areas individual outcrops are isolated by eucalypt woodland communities which are devoid of limestone.

The vine thickets on these limestone outcrops and their associated pediments are largely fire-protected. Fire appears to have been a feature of the Australian dry tropics landscape for a considerable period of time (Kershaw, 1985), but its influence has increased in intensity with the arrival of Aboriginal people more than 40,000 years ago (Singh et al., 1981) and Europeans in the last 150 years. This has complicated interpretations of environmental change based on the analyses of vegetation assemblages from pollen studies (Kershaw, 1985, 1986). However, the limestone substrate forms a natural barrier and protects the fire-sensitive vine thicket vegetation and the associated land snails. Hence climatic interpretation based on analyses of variation in shell characteristics from these environments should be relatively free of the influences of fire.

Limestone outcrops in each of these locations has been mapped by the Chillagoe Caving Club (1982, 1988, 1990) and the following brief assessments of local environments are based on these publications.

Mitchell-Palmer. The Mitchell-Palmer limestones outcrop in a series of towers running roughly in a north-south line from north of the Palmer River to the Mitchell River in the south (Fig. 1). Tower height varies, but exposures up to 150m above the surrounding landscape have been recorded (Fig. 2). Mean annual rainfall at Palmerville in the north is 1034mm; at Bellevue Station at the southern end it is 901mm, in both cases with more than 90% of the rainfall coming in the period November-April. Mean annual rain days at Palmerville = 88 (Table 1). Evaporation and transpiration exceed precipitation for eight months of the year, with the area experiencing a marked winter deficiency of water for plant growth. Towers are higher than those at Chillagoe-Mungana and include massive scree slopes (Chillagoe Caving Club, 1988).

Chillagoe-Mungana. The limestone bluffs of the Chillagoe-Mungana region are situated in a rough northwest to southeast line extending from Rookwood Station in the north, through Mungana and Chillagoe to slightly northwest of Almaden in the south (Fig. 3A). The individual towers vary from narrowly circumscribed outcrops to expansive, relatively high limestone masses (Fig. 3B). Rainfall at Chillagoe-Mungana is less than in the Mitchell-Palmer region, with the annual average around 850mm, most of which occurs between November and April (Table 2). The entire Chillagoe-Mungana region, from its northwestern to southeastern ends, can

TABLE 2. Rainfall figures for Chillagoe-Mungana region (from north to south) (Chillagoe mean mm from 1902-1998; Rookwood mean mm from 1961-1997; Almaden mean mm from 1972-1998; Chillagoe mean rain days for 1979-1982).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Rookwood mean (mm)	225	210	130	21	13	6	2	4	4	12	64	148
Chillagoe mean (mm)	210	213	141	30	14	11	4	4	5	15	56	130
Almaden mean (mm)	220	193	137	34	16	8	5	4	8	18	67	132
Chillagoe mean no. rain days	16	15	11	10	5	2	1	1	1	1	1	5



FIG. 1. Map of northeastern Australia showing areas $>600\text{m ASL}$; and distribution of limestone karst towers of the Mitchell-Palmer and Chillagoe-Mungana regions indicating locations of archaeological sites and other places mentioned in text.

be treated as a single climatic region, with variation through space being minimal. This is well illustrated by the similarities in mean annual rainfall levels for Rookwood (850mm), Chillagoe (854mm) and Almaden (852mm). Similar patterns also exist for mean monthly rainfall levels (Table 2).

The number of annual rain days in the Chillagoe-Mungana region is also less than in the Mitchell-Palmer (e.g. average for 1979-1982 = 65). A number of the limestone towers contain caves which are today the focal points of local tourism (Chillagoe Caving Club, 1982; Robinson, 1982).

PALAEOENVIRONMENTS IN NE QUEENSLAND. Most of what we know of Quaternary palaeoenvironments in northeast Queensland comes from pollen research along the eastern seaboard and the convection-affected Great Dividing Range a few kilometres to the west. Few investigations have been made in the rainshadow area to the west of the Range, an area which covers most of north Queensland where the magnitude of environmental change can be expected to be significantly less than on the Atherton Tableland and coastal regions where coastal processes are strong. Kershaw's work at various sites from the Atherton Tableland, some 150km to the southeast of Mitchell-Palmer and Chillagoe-Mungana — at Lake Euramoo, Quincan Crater, Bromfield Swamp, Strenekoff's Crater and Lynch's Crater — has revealed a series of pollen sequences covering the last 215,000 years. More recent work at the ODP 820 offshore site (Kershaw et al., 1993), Isabella Swamp, Kings Plains Lake, Garden Creek Swamp, Napabina Swamp and Barwon Swamp in the Laura region some 100km to the northeast of Mitchell-Palmer (Stephens & Head, 1995), Lake Carpentaria 500km to the west (Torgensen et al., 1988) and Ngarrabullgan some 75km to the southeast (Butler, 1998) have revealed further pollen data for palaeoenvironmental reconstructions, especially for the Holocene period. Other relevant research from tropical northern Australia and the near Pacific include works on past sea levels (Hopley, 1983; Chappell et al., 1983), oxygen isotopes on corals (Aharon, 1983), ancient charcoals and woods (Hopkins et al., 1993), cheniers (Chappell, 1982; Chappell et al., 1983), lake levels (Bowler, 1983; Torgensen et al., 1988), dunefields (Galloway et al., 1970), cave sediments (Hiscock, 1984; Hughes, 1983) and simulation studies (Nix & Kalma, 1972). Together, these studies enable us to present the

following palaeoenvironmental reconstructions for the last 40,000 years of northeastern Australia.

40,000-38,000 BP. This was a relatively wet phase, although both absolute and relative rainfall levels were probably lower than they are today. Records from Lynch's Crater indicate that the araucarian vine forests that had dominated much of the last glacial period as well as the previous glacial, were displaced by pyric sclerophyll forests dominated by *Eucalyptus*. An order of magnitude increase in charcoal peaks at Lynch's Crater coincides with this change. Given that there is little evidence for substantial climatic change around this time, Kershaw (1985, 1986) has used this change as indicating the onset of human activity, particularly burning of the landscape. The regional nature of the *Araucaria* decline is indicated by a similar sequence of events at both Lynch's Crater and the offshore ODP 820 record (Kershaw et al., 1993).

38,000-25,000 BP. Temperatures were low, but increased slightly from c.36,000 to 30,000 BP, then decreased to their lowest value sometime after 25,000 BP. Geomorphological investigations indicate that lake levels were higher than they were before c.26,000 BP. Bowler (1983) argued that this lake-full stage indicates greater rainfall (a humid expansion) around 28,000 to 26,000 BP. This is probably best explained by increases in summer rainfall. Lakes then began to contract c.25,000 BP, indicating the advent of maximum glacial activity (Bowler, 1983).

25,000-17,000 BP. The time of the Last Glacial Maximum was characterised by low effective and absolute precipitation, described as about one-third of today's levels. This was probably caused by a mixture of exposed continental shelves (drier air masses), decreased oceanic temperatures (decreased convection), and a severance of warm ocean currents from northern Australia (decreased convection) (Hopley, 1983).

17,000-8,500 BP. Effective and absolute precipitation remained low. After the height of the last glacial maximum sometime between 13,000 and 10,000 BP, however, conditions were slowly reversed. Levels of atmospheric humidity and precipitation increased with the initial flooding of the Gulf of Carpentaria c.11,000 BP, but it was not until c.8,000 BP that warm ocean currents flowed across Torres Strait (Hopley, 1983). The spatial distribution of charcoal fragments in and around present-day rainforests

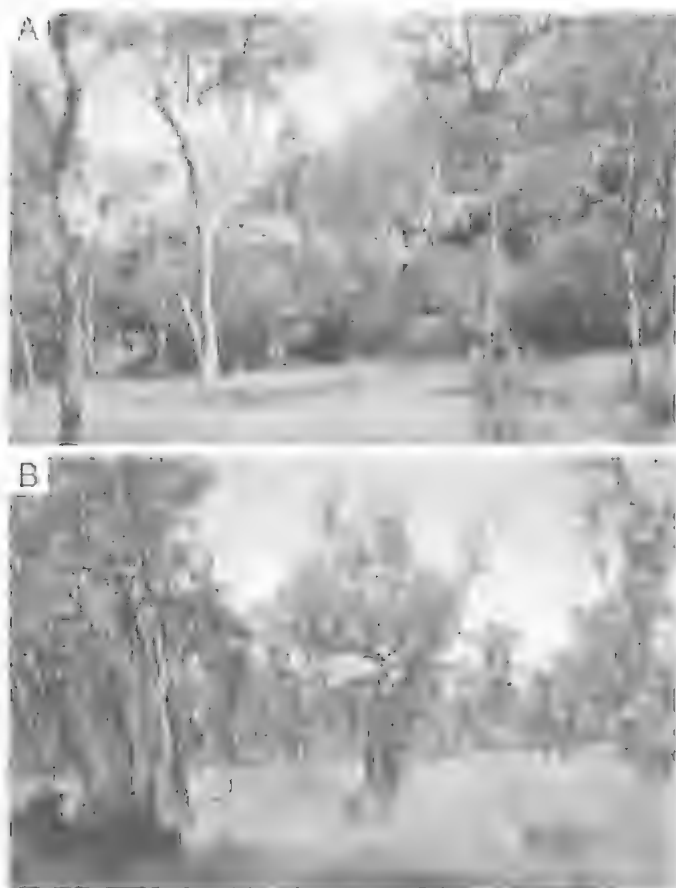


FIG. 2. Mitchell Palmer limestones. A, limestone tower and associated vine thicket. B, eucalypt woodlands surrounding the limestone towers.

suggests that the *Eucalyptus* expansion and rainforest displacement reached their maximum extents during the period 13,000–8,000 BP (Hopkins et al., 1993). By c.8,500 BP, both effective and absolute precipitation had increased to levels similar to today's; temperatures were probably also similar to those of today.

8,500–3,000 BP. This is a period of high rainfall and high temperatures. By 8,500 BP, both effective and absolute precipitation had increased to levels higher than today. Temperatures were probably similar to today. By 6,500–5,900 BP, rainfall attained levels nearly five-times those of the terminal Pleistocene on the Atherton Tableland. Explanations include an opening-up of the northern and eastern continental shelves, the creation of an eastern high energy window, the presence of convection as a result of warmer ocean currents, increased air and oceanic

temperatures and higher seas levels. Around 6,000 to 5,000 BP, sea levels were similar to today's (and possibly slightly higher), and micro-atoll and reef formations began to appear — much of the eastern continental shelf experienced reef growth and the formation of micro-atolls by around 5,000 to 4,000 BP (Hopley, 1983). The latter closed the high-energy window, slightly decreasing rainfall levels and thus effective precipitation. Palynological and sedimentary evidence from the crater lakes suggest that fire frequencies had declined and rainforest species recolonised certain areas, with rainforest achieving its maximum extent around 6,500–5,900 BP. This coincided with an increase in *Elaeocarpus* relative to Cunoniaceae and *Rapanea* pollen values. From surface sample data, *Elaeocarpus* pollen has its major representation in lower altitude forests. Bioclimatic analyses of taxa from Lake Euramoo suggest that summer temperatures may have been higher than today's, while rainfall continued to be high during winter (Hiscock & Kershaw, 1992).

3,000 BP–present. Following a lowering of absolute and effective levels of precipitation around 3,000 BP, northern Australia attained its present climatic regime. There is also

an indication from Ngarrabullgan that vegetation changed shortly after 2,000 BP from forests with a relatively dense overstorey to more open forest with a grassy understorey, and that charcoal levels in sediments increased, perhaps in response to the increased fire susceptibility of that forest type. Dry rainforest was probably present, at least in patches, due to the occasional representation of *Araucaria* pollen. From this interpretation it is speculated that the change to more open communities facilitated the onset of swampy conditions or lake formation due to increased erosion and sediment input from more exposed soil surfaces (Butler, 1998). This is in accord with the suggestion of Stephens & Head (1995) that swamp formation was widespread in southern Cape York Peninsula after 2,700 BP (but see Hiscock & Kershaw, 1992).



FIG. 3. Chillagoe-Mungana limestones. A, small outcrops; B, large tower; C, litter zone.

There is some evidence for the onset of El Niño/Southern Oscillation (ENSO) after ~7,000 BP. The evidence for changing ENSO influences in Australia is evident in past fire, drought and erosion regimes and in the stress- and disturbance-tolerant vegetation that indicate more variable climates (McGlone et al., 1992: 435). This evidence has been argued to indicate colder, drier summers than previously between 5,000 and 3,000 BP, approximating present conditions. McGlone et al. (1992) conclude that early Holocene climates were more stable than for the mid and late Holocene, pointing to 'either a much reduced amplitude of the ENSO fluctuations, or to a change in the extra-tropical expression of ENSO due to different climatic boundary conditions. It is unlikely that typical ENSO cycles were a major factor in Australasian and South American climates before about 7,000 BP, and they only began to exercise their present strong influence beginning at 5,000 and fully developed by 3,000 BP'.

In short, the record for the last few thousand years emerges as problematic. This is particularly

evident given that Stephans & Head (1995) have proposed that water levels have been more reliable in the last 2,700 years, while Hiscock & Kershaw (1992) nominate driest Holocene conditions occurred between 2,600 and 1,400 BP. The disturbance of upper sediments within pollen sites is suggested as one possible explanation (Stephans & Head, 1995). However, such discrepancy more likely implies not a single discrete period of changed environmental conditions but increased climatic variability during the last 3,000 years, with short periods of decreased wet season rainfall (Lees et al., 1992). As noted above, some studies (McGlone et al., 1992; Shulmeister & Lees, 1995) have gone further, arguing for the onset of ENSO from the mid Holocene. Australian droughts generally coincide with El Niño events, a relationship most consistent over eastern and northern Australia, while prolonged, heavy rainfall and consequent floods accompany the reverse cycle known as La Niña. The general effect of these events is to increase rainfall variability across the continent and through time (McGlone et al., 1992).

INVESTIGATING PALAEOENVIRONMENTS IN NORTH QUEENSLAND VIA LAND SNAILS

While some land snail taxa, such as *Vertigo* spp. in Europe (Evans, 1972) and *Subzebrinus cremitus* in Afghanistan have been used as indicators of past changes in moisture levels, comparatively few detailed studies have ever been made of the response of particular shell characteristics to specific climatic or environmental factors (see Goodfriend, 1986 for summary).

David & Stanisc (1991) used the total land snail assemblage from an excavation at Echidna's Rest, tropical northeastern Queensland (Fig. 1), to make broad-scale regional interpretations of environmental change in the Chillagoe region, and also emphasised that individual species may yield useful micro-environmental data. Much of our understanding of the alternation of wet and dry phases since the late Pleistocene has been gained from pollen analyses of sample cores from lacustrine environments relatively close to the eastern seaboard (e.g. Kershaw, 1970, 1971, 1975, 1976, 1985). However, while this pollen work has revealed extremely long and more or less continuous sequences, some spanning hundreds of thousands of years, palaeoclimatic and palaeoenvironmental conditions for some periods of time and for some modern biogeographic zones are better understood than others.

One deficiency that is particularly problematic for archaeologists is a paucity of such data for the period 17,000 to 10,000 BP. This poorly understood period of time is compacted in the pollen sequences studied so far, particularly at the major pollen site of Lynch's Crater (Kershaw, 1974, 1976, 1994). Elsewhere in Australia, the palaeoenvironmental evidence is clear and consistent, indicating sustained rainfall rises after the last glacial maximum at various times after 17,000 BP. In northeastern Queensland, however, the existing pollen evidence for this period, while of poor temporal resolution and dubious stratigraphic quality, implies that annual rainfall levels may not have increased until ~13,000, and perhaps even as late as 10,000 BP. Indeed, terminal glacial aridity may have been greatest around 13,000 BP (Kershaw, 1994). A determination of the timing of increased rainfall in this region has major implications for archaeological reconstructions. For example, Lamb (1996) and David & Chant (1995) argued

that people were restricted to a few sources of surface water during the dry season in the Chillagoe region during the last glacial maximum, broadening their territories and altering systems of land use as conditions became wetter and biomass increased after ~17,000 BP. Evidence for such changes in cultural behaviour is evident at Fern Cave near Chillagoe, and possibly at Hay Cave in the Mitchell-Palmer limestone zone to the north where large, permanent and apparently long-standing springs can be found. However, if rainfall levels did not begin to increase until well after people had already abandoned these places and/or broadened their lived horizons, alternative models of change in settlement behaviour – specifically site and regional land use – and cultural dynamics relative to environmental conditions would have to be considered. Unfortunately, appropriate pollen sites are rare in these regions, and sedimentation rates across the landscape are generally very slow, rendering suitable palaeoenvironmental indicators outside of caves hard to find.

The shells of land snails from archaeological excavations within this region, particularly those which span the period from the last glacial maximum to present, would appear to be capable of providing the information necessary to address such questions – especially if sufficient numbers could be recovered for size analyses. Their presence within caves and rockshelters, where sedimentation is usually varied but more or less continuous, affords us the possibility of obtaining stratified sub-fossil assemblages covering relatively long periods of time. Land snails could thus act as an independent test for existing palaeoenvironmental trends, as well as perhaps also providing a finer level of detail than pollen analyses are capable of achieving. Pollen sequences are often limited to evidence of genus or higher-order changes in community composition. Vegetational changes affecting the species or sub-species often fail to register in the pollen record. This is particularly problematic in Australian semi-arid conditions, where *Eucalyptus*, *Acacia* and *Melaleuca* tend to predominate the upper storeys. Under such circumstances, changes in species composition are rarely identifiable from the pollen record, unless a genus or higher-order taxonomic change also takes place. However, some environmentally sensitive species of land snails may be able to overcome this limitation. The Echidna's Rest study identified the helicimid *Pleuropoma*

extincta (Odhner, 1917), which is a prosobranch gastropod, as a likely candidate for such analyses.

Prosobranch gastropod land snails, such as *P. extincta*, are more appropriate environmental indicators than pulmonates. They have an open pallial cavity rather than a closed lung, suggesting that these species are much more liable to respond to environmental moisture changes than is the case with pulmonates (Solem, 1991). In the latter the lung can be used as a 'water-bag' for storing moisture, thus potentially ameliorating the effects of dry climatic phases, both spatially and temporally. This greater sensitivity to changes in environmental moisture regimes could be expected to reflect in more easily detectable size changes in the shells of these animals. The underlying rationale is that as rainfall patterns and microenvironmental humidity levels vary, so will activity periods which determine growth rates.

Hence the usefulness of *P. extincta* in palaeo-environmental reconstruction is dependent ultimately on two main factors: firstly, the capacity to show that this species does in fact respond to environmental moisture change (in time and space) in a way that can be easily measured and analysed; and secondly, the ability to recover sufficient undamaged material from an archaeological or palaeontological excavation with an extended and finely calibrated temporal sequence. The latter problem involves not only questions of site preservation, but also of excavation methods.

PLEUROPOMA EXTINCTA: ECOLOGY AND DISTRIBUTION. In many land snails moisture-related responses are reflected in changes in shell patterns which can be measured. These include size, whorl number and shell thickness, although in the latter the correlation has yet to be thoroughly studied (Goodfriend, 1986). While other factors — such as temperature, insolation, the availability of calcium and population density — are also known to affect shell size, moisture appears to be the best documented factor (Goodfriend, 1986) and has been the basis of several detailed studies (Tillier, 1981; Gould, 1984) which suggest that it perhaps is a critical factor in determining both size and shape differences within species and between populations. Considering the acute moisture sensitivity of land snails, such a conclusion would seem appropriate. However, given the relative lack of studies in this sphere

and the inconclusive nature of some, it is not possible to accept the universality of the moisture-size relationship and each case must be assessed separately. It also needs to be kept in mind that though the size of shells is determined by whorling pattern, shells can become large in two ways: few large-sized whorls or many small-sized whorls (Gould, 1984). However, a strong positive correlation between size and whorl count may also indicate that size increase is purely a function of whorl count increment without any appreciable change in whorl size. Hence, determining the shell parameter which will be most useful as an index of moisture levels also becomes a crucial consideration.

LAND SNAILS IN SEASONAL ENVIRONMENTS. Environmental moisture-related variation in the shell size of Australian land snails has been reported by Solem & Christensen (1984) for camaenids from the vine thickets of the Kimberley and inferred for a number of non-camaenids from other seasonal environments in tropical northern and northwestern Australia (Solem, 1982; 1984). In each of these cases the implication was that variations in shell size correlated with differences in whorl numbers of adult shells and that they were not merely due to variations in overall size wherein large shells result from larger animals with larger whorls and vice versa. Furthermore, Solem (1991) suggested that shell-size variation in populations of *Pleuropoma walkeri* (Smith, 1894), a helicimid from the vine thicket patches of northwestern Australia, may also be a reflection of differences in local moisture conditions, although no analysis was undertaken. This latter inference has significant implications for using *P. extincta* in fine-grain palaeoenvironmental reconstruction.

Reasons for the size differences in the shells of the land snails from these monsoonal (= seasonal) environments relate directly to the nature of the climate and the specific adaptation of the local snails to this climate (Solem & Christensen, 1984; Solem, 1988). These land snails have the capacity to vary in adult shell size because of variations in the length of feeding activity available during growth from juvenile to adult (Smith & Stanisic, 1998). This feeding activity is related to intensity and duration of summer rainfall ('the wet'), and since these snails appear to reach adulthood synchronously at the end of their second wet season (Solem, 1982; 1984), maturity can lead to adults with different whorl numbers depending on the quality of the growing

seasons. However, it also needs to be noted that while rainfall results in growing activity, this response is not always a simple function of annual rainfall or annual number of rain days. Rather, land snail activity periods during and after significant 'activating' rain events vary according to the complexity of local environmental conditions, which include such factors as vegetation cover, topography and geology (Solem, 1988).

The Chillagoe-Mungana and Mitchell-Palmer limestone outcrops (Fig. 1) are part of this archipelago of seasonal environments and receive most of their rainfall in a relatively short time during summer (see above).

The land snail faunas of limestone areas in eastern Australia are comparatively rich when compared with the snail fauna of the surrounding non-limestone areas (Stanisic, 1994; 1997a,b). However, while the diverse nature of the fauna in some of these areas has been documented (Stanisic, 1997c), many of the taxa have yet to be formally described. The land snails of the limestones of the Chillagoe Formation are no exception. Odhner (1917) described the first species from Chillagoe and since then only a few extra species have been added (Iredale, 1937, 1938). Their classification and distribution are summarised in Smith (1992). Stanisic (1997d) briefly detailed and illustrated the land snail fauna of the Chillagoe-Mungana limestones, including undescribed species, and drew attention to its diverse make-up of widespread and locally endemic taxa. The equally prolific Mitchell-Palmer land snails are largely undocumented, though they are well represented in the collections of the Queensland Museum.

These two limestone areas share a number of taxa, including *P. extincta*. This species displays shell size variation across the range of its occurrence (Stanisic, unpubl.). *P. extincta* has also been recovered from archaeological excavations at Hay Cave, towards the northern end of the Mitchell-Palmer limestones (Fig. 7). Radiocarbon dates associated with cultural remains from this cave suggest a temporal sequence covering the last ~19,000 years at least, a time period which spans a number of major wet/dry climatic phases in the region.

These circumstances provide an opportunity to examine the extent of shell variations in recent *P. extincta* and to see whether these have palaeo-environmental implications.

Pleuropoma extincta (Odhner, 1917). The shell of *P. extincta* is small (adult size: diameter 2.3-6.6mm, height 2.0-5.4mm), top-shaped and sculptured with numerous spiral cords; the periphery is angulate, there is no umbilicus and the shell is relatively thick (Fig. 4). Its small size and relatively thick walls make *P. extincta* shells capable of withstanding relatively high levels of chemical and mechanical weathering, an important consideration when investigating buried sequences. *P. extincta* is comparatively widely distributed (N-S approximately 175km) in the Einasleigh Uplands Biogeographic Region, but it is environmentally restricted (Stanisic, unpubl.). It appears to live exclusively on the limestones of the Chillagoe Formation (Fig. 1). The species was mistakenly recorded from a tiny patch of vine thicket in the Mt. Mulligan area, northeastern Queensland by Stanisic & Ingram (1998). While the Mt Mulligan population is superficially similar to *P. extincta*, recently obtained anatomical details show that it is a different species (Stanisic, unpubl.). *P. extincta* is an obligate vine thicket dweller (Fig. 2A) and has not been recorded from the more expansive eucalypt forest/woodland communities which dominate much of this region (Fig. 2B). It is also absent from the vine thickets growing on the massive lava flows which occur in the surrounding countryside, such as at Undara and Kinrara to the south. The latter habitats are occupied by another, undescribed species of *Pleuropoma* (Stanisic, unpubl.). Present-day distribution of *P. extincta* is the result of long-term, climatic changes which have also affected the distribution of vine thicket communities (Stanisic, unpubl.). Because of their enhanced ability to retain ground moisture, vine thickets associated with the limestone pediments act as refugia for *P. extincta* and other micro-organisms during dry phases. *P. extincta*'s current restriction to these habitats is indicative of its past and present sensitivity to regional and local moisture regimes.

P. extincta lives chiefly under strewn limestone talus, on leaves and bits of timber in the litter and on the trees which grow on these outcrops. It may also occur on the limestone rock where it seals itself to the karst surface in the many cracks and crevices. Compared with most other land snails on these limestones, it is present in very high numbers. *P. extincta* is not subterranean but may occur around the entrance of caves. It does not burrow, an important consideration when analysing subsurface, sub-fossil assemblages. Its

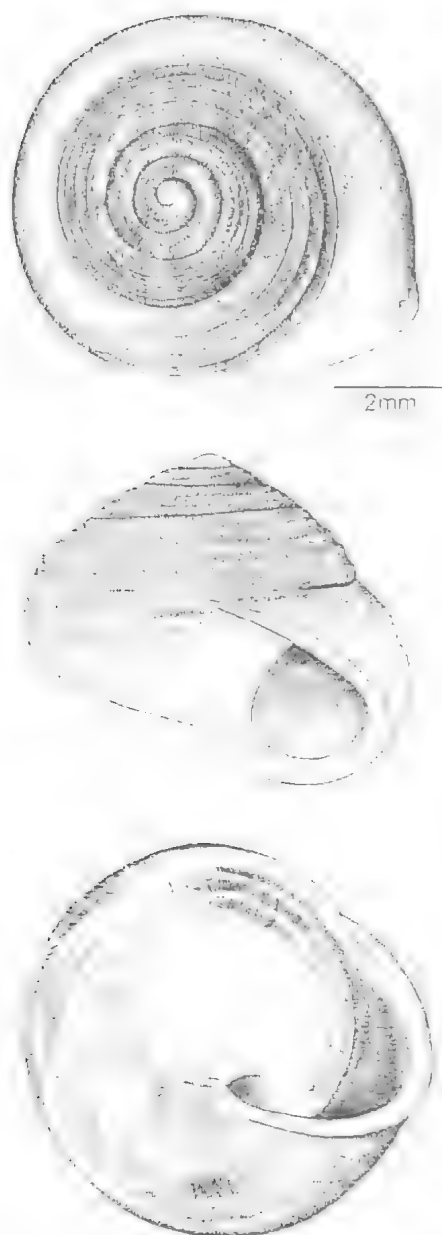


FIG. 4. Shell of *Pleuropoma extincta*. [A. Francis].

presence in great numbers along drip points within caves is probably a result of the removal of finer, surface sediment particles by percolating water, concentrating larger particles (including snail shells) in exposed pockets. Because of their large numbers in living populations and the alkaline nature of the environment, dead shells also accumulate in the litter in great abundance (Fig. 3C).

MATERIALS AND METHODS

Recent specimens of *P. extincta* came from the collections of the Queensland Museum (QMMO). Methods comprised hand-collecting specimens and specimen-containing leaf litter from various limestone outcrops, including the ground surfaces of cave entrances and interstitial spaces between rocks and boulders on talus slopes. The shells were subsequently separated from the leaf litter by hand-sorting in the laboratory. Shells retrieved from leaf litter represented the accumulation of several years of dead individuals. The ability to sample land snails *post-mortem* greatly enhances their utility in environmental interpretation.

Preliminary analysis of samples involved separation of individuals into three categories: adult or juvenile, based on the thickness of the outer-lip (peristome), and unclear according to the degree of coating of calcium carbonate. Each sample category was counted, totalled and labelled. To facilitate measurement 10 adult *P. extincta* shells were placed at a time on the stage of a calibrated dissecting microscope (Zeiss 475052-9901) and observed by reflected light under $\times 12$ magnification. The parameters measured were whorl count, height and diameter. Of those that were partially broken or damaged, it was only possible to measure one or two of the three variables. These damaged specimens were also counted and labelled.

Shell height was measured from the apex to the base of the aperture, and diameter covered the lateral span of the body whorl. These observations were recorded to the nearest 0.05mm. Measurements beyond 5.00mm were performed with a dial calliper (Mitutoyo 505-667 D20F), accurate to 0.01mm. Calculation of whorl number was coordinated by aligning the origin of the whorl pattern at the apex in the vertical position and counting to the nearest eighth rotation (Solem, 1976).

STATISTICAL ANALYSIS. The mean value for each parameter within each outcrop unit sample was calculated to a single standard deviation. In this way, statistical comparisons of parameters from different sites were possible. In each analyses the range of measurements was noted for each character.

For convenience of data presentation and interpretation, variations within shell characteristics are presented as scatter-graphs of diameter vs. whorl count, height vs. whorl count and height vs. diameter. Such statistical analyses

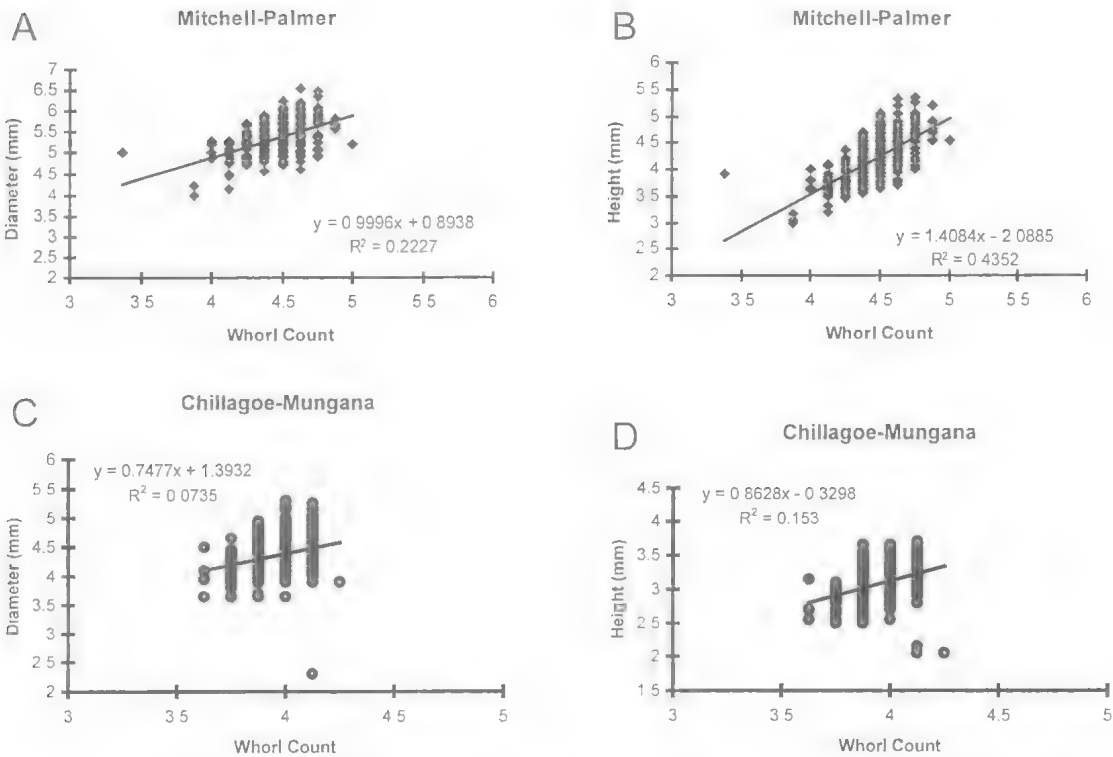


FIG. 5. Surface collections (control samples), *P. extincta* statistics (with simple regressions). A, whorl count versus diameter (mm), Mitchell-Palmer; B, whorl count versus height (mm), Mitchell-Palmer; C, whorl count versus diameter (mm), Chillagoe-Mungana; D, whorl count versus height (mm), Chillagoe-Mungana.

were first undertaken for each individual sample set (i.e. samples from individual limestone outcrops). In order to investigate spatial patterning in shell height, diameter and whorl count within a regional framework, adult data were pooled into a combined Chillagoe-Mungana dataset, and into a Mitchell-Palmer dataset. To describe and quantify the relationship between the parameters, and determine the strength of any possible correlation, a simple regression analysis and associated equation is provided for each graph.

In addition, to allow for an understanding of the relationships between the parameters for the entire study and determine the correlation strengths at this scale, all regional data were combined on a single graph. This technique therefore used all measured variables in the one analysis. Here, the regressions were second-order polynomial to account for the presence of two regional populations (Chillagoe-Mungana and Mitchell-Palmer).

RECENT PLEUROPOMA EXTINCTA

Analysis of shell variation (Tables 3-5). Average largest shells and highest average whorl counts occur among the Mitchell-Palmer material (Fig. 5A,B).

When the Mitchell-Palmer and Chillagoe-Mungana areas are treated together, whorl count depicts strong positive correlation with height and diameter (correlation coefficient ~0.72-0.83; Fig. 6A,B). When each region is treated in isolation, however, the strength of this relationship is not as evident (Fig. 5A-D), with the correlation coefficient failing to exceed 0.44. This latter poor correlation is also evident when each collection area was analysed as a separate

TABLE 3. Range of variation in *P. extincta* (mean, sem and range).

Locality	No. of specimens	Height (mm)	Diameter (mm)	No. of whorls
Chillagoe-Mungana	602	3.075±0.224 (2.05-3.70)	4.344±0.280 (2.30-5.30)	3.947±0.101 (3.625-4.250)
Mitchell-Palmer	542	4.205±0.353 (3.00-5.35)	5.361±0.350 (4.00-6.55)	4.468±0.165 (3.375-5.000)

TABLE 4. Local variation in *P. extincta* from Mitchell-Palmer area (mean, sem and range).

QM Reg. no.	No. of specimens	Mean height (mm)	Height range (mm)	Mean diameter (mm)	Diameter range (mm)	Mean whorl count	Whorl count range
MO22998	5	3.110±0.119	3.00-3.30	4.150±0.087	4.00-4.20	3.925±0.112	3.875-4.125
MO23375	72	3.844±0.019	3.45-4.20	5.179±0.226	4.75-5.80	4.377±0.159	4.000-4.750
MO23388	7	3.950±0.515	3.20-4.70	4.850±0.420	4.45-5.60	4.464±0.310	4.125-4.875
MO23584	29	4.036±0.202	3.65-4.45	4.984±0.234	4.55-5.35	4.401±0.158	4.125-4.750
MO23592	7	4.150±0.367	3.65-4.65	5.529±0.438	4.90-6.10	4.482±0.152	4.250-4.625
MO61156	208	4.148±0.249	3.60-4.85	5.285±0.243	4.70-5.95	4.468±0.134	4.125-4.875
MO61172	24	4.381±0.210	3.85-4.70	5.427±0.251	5.00-5.85	4.531±0.129	4.250-4.750
MO61191	87	4.342±0.262	3.80-5.05	5.452±0.222	4.95-5.90	4.476±0.180	3.375-5.000
MO61205	103	4.529±0.317	3.95-5.35	5.735±0.294	5.00-6.55	4.557±0.123	4.250-4.875

outcrop unit. In terms of variation, the whorl counts, diameters, and heights of shells from any one region, single limestone outcrop unit or individual collection unit appear smaller; the spread between the values becoming narrower, forming a cluster, rather than distinct linear spread, on the graph. Relating this to analytical scale, the positive correlation between whorl count and size of the shells is thus illustrated at the inter-regional level and does not arise at a more local scale. This patterning is also visible in the geographical pattern of rainfall variation, which is fairly marked at the inter-regional level, but not at a local scale. This correlation implies that the relationship between whorl count and diameter or height is likely to be extrinsic rather than intrinsic. It implies that the relationship between whorl count and diameter or height requires variation in environmental influence(s) on these variables. This is consistent with findings of strong environmental, and in particular humidity, influences on whorl growth (see above). Highest whorl counts, calculated as % of total numbers of individuals occupying various whorl count classes, shows the Mitchell-Palmer specimens to be consistently higher than those at Chillagoe-Mungana (Table 3).

ENVIRONMENTAL INTERPRETATION. Differences in mean shell size between the Mitchell-Palmer and Chillagoe-Mungana material correlate positively with differences in local rainfall regimes. On average the Mitchell-Palmer specimens are larger than Chillagoe-Mungana ones, which has lower average annual rainfall. Although larger shell size can result from a number of other factors, such as temperature, insolation, calcium availability, population density and soil pH, their effects were not measured. Studies elsewhere have linked some of these factors with differences in whorl

expansion rates, shell weight, diameter and height (Bengston et al., 1979; Owen, 1965). In most instances, differences in shell size were related to differences in whorl cross-section.

Goodfriend (1986) presented several hypotheses to explain the relationship between these environmental variables and adult shell size. However, in most cases the differences were in connection to the initial size of the whorls and the rate at which the whorls expanded — that is, the aperture and whorl cross-sectional area (=whorl volume). In this case, variation in aperture and whorl cross-sectional area do not represent a similar function to the number of whorls, but they are generally interpreted as representing either an adaptation for regulation of water loss, to reduce predation, or both. They are, therefore, not as dependent on the surrounding habitat (Goodfriend, 1986).

In the context of this study, the strong positive correlation between whorl count and both diameter and height in *P. extincta* indicates that size differences in this species have an affinity to variations in whorl 'count' rather than whorl 'size'. These findings coincide with the camaenid land snail growth patterns in semi-arid areas of northwestern Australia as discussed by Solem & Christensen (1984). Adult shell size in their study is seen to depend upon moisture conditions near the end of the snail's second wet season. An early interruption of moisture supply causes growth to stop at a lower whorl count and produces smaller adults. Favourable moisture conditions allow extended growth time, with cessation occurring at a higher whorl count, and producing a larger adult size (Solem & Christensen, 1984). What Solem & Christensen (1984) implied is that the regular and predictable wet season in the Kimberley region is the key to understanding the maturation pattern of its land snails. The length of

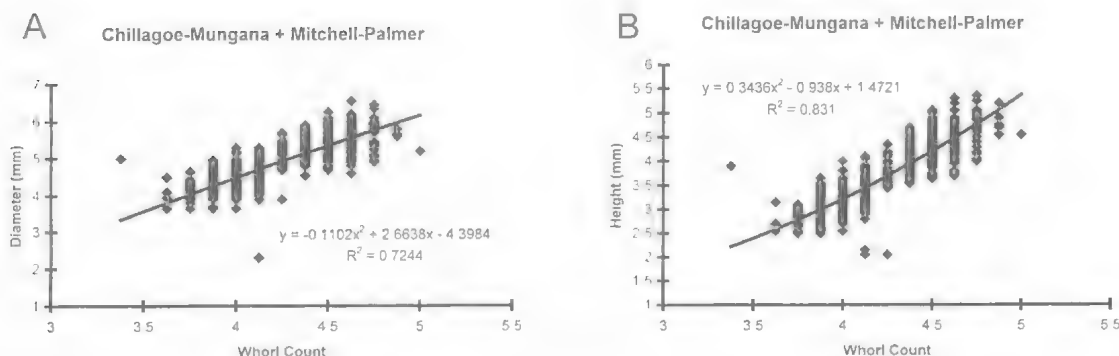


FIG. 6. Mitchell-Palmer + Chillagoe-Mungana. A, whorl count versus diameter (mm); B, whorl count versus height (mm). Regressions are second-order polynomial, to take into account the presence of two regional populations.

the wet season may vary from as little as two months on the southern fringes, to as long as six months in the Mitchell Plateau. The median wet season rainfall is only 500mm near Fitzroy Crossing and Halls Creek, but nearly 1600mm on the Mitchell Plateau. These parameters define the potential maximum length of the activity period for the snails (Solem & Christensen, 1984).

The lower number of rain days at Chillagoe-Mungana compared to the Mitchell-Palmer appears to at least partially account for the smaller-sized (= lower whorl count) snails. Given this, whorl count in *P. extincta* appears to be a useful indicator of differences in regional rainfall levels, which in turn suggests that this shell feature may also be a useful index of change in past environmental moisture levels along the limestone belt of the Chillagoe Formation. Evidence indicating the sensitivity of *P. extincta* to environmental moisture levels is strengthened through the presentation of initial findings highlighting little intra-regional variation, where each outcrop has a fairly uniform rainfall pattern. However, the most significant correlation between size and whorl count is between regions with perceptible differences in mean annual rainfall levels.

In contrast to the above, Solem & Christensen (1984) concluded that the pattern of size variation in land snails in the Kimberley region was very much a local phenomenon dependent on both moisture regimes and microhabitat. Populations of *Westraltrachia* at Wombarrella Gap differed by up to 3mm in mean adult diameter over distances of less than 100m. The small shells were collected near a single isolated boulder, and the larger specimens were taken in shaded talus

that would retain moisture for a longer period of time (Solem & Christensen, 1984).

Although the north Queensland results do not show the strong patterns of local variation seen in some Kimberley species it should be borne in mind that the recent material was mostly collected from large karst towers whose micro-topography was generally considered to be similar. There are however, tantalising indications that local influences would be worth further investigation and that outcrop size and aspect may also play a mitigating role in final shell size of *P. extincta*. For instance, material from Mitchell-Palmer sample QMMO22998 was collected from a small, low relief outcrop and has comparatively smaller whorl counts and size than others from the region (Table 4). Specimens from Royal Arch Caves, Chillagoe-Mungana (QMMO53436) displayed the largest size and whorl counts for specimens from this region (Table 5). While this limestone outcrop does not demonstrate any apparent physical differences to others from the region, the land snail assemblage does suggest that it has intrinsic differences. The large camaenid land snail, *Spurlingia praehadra* (Odhner, 1917), occurs almost exclusively on this outcrop indicating that it probably is somehow environmentally distinctive. Further research on these aspects appears warranted because if these casual perceptions about local differences in *P. extincta* are related to local habitat differences, then the role of *P. extincta* as a useful indicator species would be enhanced.

APPLICATION TO AN ARCHAEOLOGICAL ASSEMBLAGE: HAY CAVE

Hay Cave is located towards the northern end of the Mitchell-Palmer limestone belt, near

TABLE 5. Local variation in *P. extincta* from Chillagoe-Mungana area (mean, sem, range).

QM Reg. no.	No. of specimens	Mean height (mm)	Height range (mm)	Mean diameter (mm)	Diameter range (mm)	Mean whorl count	Whorl count range
MO15955	9	3.067±0.224	2.70-3.40	4.411±0.204	4.00-4.65	3.931±0.110	3.750-4.125
MO19527	85	2.968±0.220	2.05-3.40	4.189±0.208	3.65-4.60	3.891±0.107	3.625-4.250
MO25996	40	3.111±0.195	2.55-3.55	4.328±0.186	4.00-4.75	3.931±0.109	3.750-4.125
MO38499	6	3.100±0.148	2.90-3.35	3.975±0.829	2.30-4.45	3.979±0.094	3.875-4.125
MO50229	15	2.823±0.231	2.50-3.40	4.173±0.171	3.90-4.45	3.908±0.088	3.750-4.000
MO50231	19	3.324±0.197	2.95-3.65	4.616±0.242	4.00-4.95	3.961±0.094	3.750-4.125
MO53325	31	3.148±0.166	2.80-3.45	4.574±0.237	4.20-5.15	3.948±0.090	3.750-4.125
MO53335	19	3.005±0.222	2.70-3.50	4.363±0.309	3.90-4.95	3.888±0.109	3.750-4.125
MO53436	25	3.452±0.154	3.20-3.70	4.910±0.194	4.60-5.30	4.070±0.063	4.000-4.125
MO53448	20	2.860±0.240	2.15-3.20	4.050±0.145	3.65-4.25	3.944±0.137	3.625-4.125
MO53551	21	3.060±0.119	2.90-3.30	4.400±0.152	4.15-4.65	3.929±0.075	3.875-4.125
MO53564	20	3.063±0.143	2.85-3.40	4.310±0.136	4.05-4.55	4.013±0.099	3.875-4.125
MO58485	220	3.116±0.184	2.05-3.40	4.386±0.216	3.80-5.00	3.953±0.089	3.750-4.125
MO58540	31	2.947±0.158	2.65-3.35	4.074±0.145	3.70-4.40	3.948±0.063	3.875-4.000
MO58547	41	2.985±0.174	2.60-3.45	4.237±0.164	3.90-4.55	3.976±0.098	3.750-4.125

Palmerville Station. Mean annual rainfall is estimated to approximate 1,034mm given its proximity to the station. It is a medium- to large-sized cave positioned at the base of a large limestone tower. The site's entrance is located at an estimated 2m above the surrounding plains. The area outside the dripline displays evidence of roof collapse in the form of numerous boulders. Boulders caused by roof-fall are also present inside the dripline in some cave chambers, but never in the central area of human occupation, where the excavation was undertaken. The cave entrance is itself not visible from the outside, as it is hidden by a thick web of vine thickets. These circumstances lead to a lack of direct sunlight reaching the cave, and consequently a relatively constant, cooler and humid internal climate.

Evidence of human activity includes a massive boulder whose edges have been flaked and numerous paintings that occur from the entrance to the very back of the cave, a distance of approximately 17m. The central part of the cave possesses soft, ashy floor deposits, signalling the presence of ancient fireplaces below ground.

FIELD AND LABORATORY METHODS. Hay Cave was excavated by BD and HL as part of an Earthwatch-funded project in mid 1996 (Fig. 7). The reasons for the excavation were multiple, focusing on human responses to environmental change in north Queensland during the last glacial maximum (in particular the period 21,000 to 13,000 BP). Four juxtaposed 50 × 50cm squares (test pits), forming a 1 × 1m square

matrix, were excavated. Excavation commenced near the central zone of soft ashy surface deposits where sediments appeared to be deepest (and potentially oldest) and least disturbed by animals and water. The 4 test pits were labelled M30, M31, N30 and N31. Square M30 proved to be the deepest square excavated and the focus of subsequent investigations.

Excavation methods employed ~2cm excavation units (XU) within stratigraphic units (SU). This method simply recognises that sediments have in the past accumulated progressively, at times resulting in the formation of distinct strata. Excavation units are employed during excavation because sediments of similar composition may have accumulated over long periods of time, so that a single stratigraphic unit may represent many hundreds or even thousands of years of sediment accumulation. Excavation units thus enable the excavator to sample different parts of a given stratigraphic unit, enabling an investigation of its internal structure and contents.

Major changes in sediment colour, texture and observable content at the time of excavation and section description were deemed separate SU: minor stratigraphic changes were identified as changes in sub-layers. The SU were numbered sequentially from top to bottom, with sub-layers characterised by an alphabetical letter after the SU number (e.g. SU2a and SU2b). The location of all cultural material measuring over 2cm maximum diameter and observed in situ was



FIG. 7. Hay Cave.

recorded in three dimensions, plotted on recording forms and bagged separately. The remaining sediments were weighed, dry-sieved in 3mm-mesh wire sieves and bagged for subsequent sorting. In the laboratory, this material was later wet-sieved, air-dried and sorted. Sorted sediments thus resulted in various components for each XU, including stone artefacts, bone, mussel shells, land snails and calcium carbonate (CaCO_3) concretions. Sediment samples from the <3mm residue were collected from each XU from each square along with pH readings. Pollen and oriented sediment micromorphology samples were also collected

from the pit walls upon completion of the excavation.

Dating. Eight samples for radiocarbon dating were extracted from square M30. Seven of these dates were derived from charcoal; the remaining OZD-012 determination was on freshwater mussel shell. All samples were collected *in situ* from the upper two SU where sediments were relatively easy to dig. These radiocarbon dates were obtained from various parts of the square, covering much of the sequence. The charcoal and mussel shell were pre-treated for possible rootlet and carbonate contamination by the radiocarbon laboratories before dating. Sample Wk-6053 was sent to the University of Waikato Radiocarbon Laboratory (Hamilton, New Zealand). All other samples were forwarded to ANSTO (Physics Division, Lucas Heights Research Laboratories, Australia). The former date is a conventional radiocarbon determination, the latter by accelerator mass spectrometry (AMS) (Table 6).

Microscopic and statistical analysis of excavated materials. The segregation of materials from the excavated sediments provided a useful opportunity to identify changes in the relative proportions of components. This allowed the

TABLE 6. Radiocarbon dates from Hay Cave.

XU	Depth (cm)	Age (BP)	Lab no.
XU2	1.4	350±55	Wk-6053
XU6	8.0	660±75	OZD-006
XU12	17.1	870±65	OZD-007
XU26	46.0	2,590±80	OZD-008
XU34	64.0	3,100±60	OZD-009
XU45	91.0	13,450±150	OZD-011
XU49	102.8	13,600±180	OZD-422
XU56	118.2	19,300±140	OZD-012

quantity of deposited land snail shell to be graphed according to excavation unit. A similar method was employed to graph the frequency of CaCO_3 concretions. In turn, the *P. extincta* shells were separated in an equivalent manner to the modern collections, enabling the number of specimens deposited per unit time to be calculated. Shell measurements and statistical analysis were undertaken in the same manner as employed in the modern samples. The mean whorl count, height, and diameter from each excavation unit were outlined on three graphs. Low *P. extincta* counts in some XU highlighted a need for caution in interpretation, and consequently neighbouring XU with under 10 specimens were combined to increase sample size. A third order polynomial regression was super-imposed on the graphs. This choice of regression type reflects the aim of investigating long-term environmental change, the nature of variation within the data and the possible representation of three major climatic regimes for the period in question, as informed by pre-existing palaeoenvironmental research. Trends in shell characteristics were then identified through time.

RESULTS. Radiocarbon determinations (Table 6) of age range from c.19,300 to c.350 years BP, and a precision of one standard deviation is given for each. All dates are in sequence.

Deposition of sediments within Hay Cave. There is a high incidence of land snail shells by weight (all species combined, but consisting mainly of large *Hadra* aff. *bipartita* and *Xanthomelon pachystylum*) from 13,600 BP to around or shortly before 3,100 BP (XU49-XU38) (Fig. 8). This incorporates a peak of 688.0g at XU40. Prior to this time, total shell weights are comparatively low. Above XU38, a pronounced decrease to almost negligible levels is evident, encompassing the period 3,100 BP-present (XU33-XU1). The highest incidence of CaCO_3 concretions in Fig. 9 corresponds in timing with the period of peak land snail shell deposition, between 13,450 BP and 3,100 BP (XU45-XU34).

Deposition rates of *P. extincta* shells per 100 years (Table 7) reveal two major depositional regimes: one before approximately 3,100 BP (XU56-XU35) characterised by significantly low shell frequencies, and the other since 3,100 BP (XU34-XU1), when numbers are some 20-fold higher.

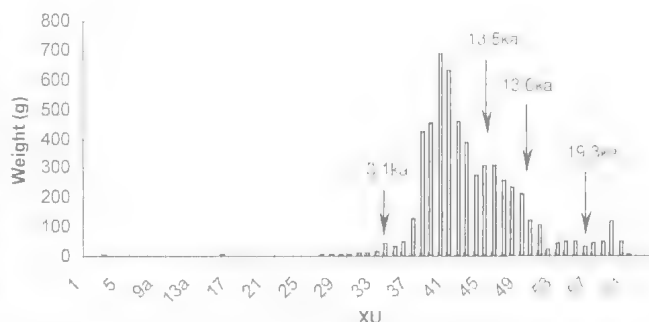


FIG. 8. Land snail shell excavated from square M30, Hay Cave: total land snail shells by XU.

Pleuropoma extincta at Hay Cave. A total of 295 *P. extincta* shells were recovered from excavation square M30 at Hay Cave. Most (236) are adult specimens, with 59 at undetermined stages of maturity given the presence of CaCO_3 encrustation or breakages effectively removing or hiding characteristic features. Of the adult specimens, 17 were partially broken. This left 219 specimens where each of the three measurements — height, diameter and whorl count — could be made.

Mean whorl counts, heights and diameters by excavation unit at Hay Cave are represented in Fig. 10. A description of relationships is based on the shapes of the regression curves, which display similar trends but are not identical to each other. Of the three represented graphs, mean whorl counts demonstrate minor variation across the time span, indicating slight decreases from an under-pronounced peak at 13,600-13,450 BP (XU49-XU45). Values change little from about 3,100 BP (XU34) until 660 BP, after which they decline further to 350 BP (XU2) and present levels. However, variability between individual samples through the sequence is high.

TABLE 7. Deposition rates of *P. extincta* numbers per 100 years at Hay Cave (note that XU45 to XU49 were not separated as dates were within one standard deviation of each other).

XU range	No. of shells	Duration in years	No. shells/100 years
XU1 - 2	27	350	7.71
XU3 - 6	33	310	10.64
XU7 - 12	32	210	15.24
XU13 - 26	89	1720	5.17
XU27 - 34	59	510	11.57
XU35 - 49	53	10,500	0.50
XU50 - 56	1	5700	0.02

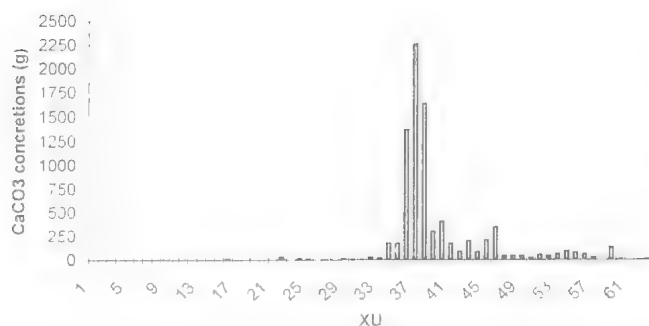


FIG. 9. Total weight of calcium carbonate concretions excavated from square M30, Hay Cave, by XU.

Mean heights show more extreme variation of the trends evident in whorl counts, expressing a greater decrease through the last 660 years (XU6-XU2) and indicating an obvious peak at 13,600 BP (XU49). This peak is followed by a marked decrease through the period 13,450-2,590 BP (XU45-XU26) and a rise to a lower peak at 660 BP.

The trend for mean diameter is similar to that for mean height. This tendency was generally expected given that height showed strong correlation with diameter in the Mitchell-Palmer and Chillagoe-Mungana control study. The *P. extincta* shells dating to 13,600 BP (XU49) correspond to peak levels, decreasing to relatively small measurements from 3,100 to 2,590 BP (XU34-XU26). Diameters rise to a second, almost equal peak through the period 870-600 BP (XU12-XU6), after which they decrease to low levels. As with mean height, variability between individual samples is high.

DISCUSSION. Major temporal phases can be identified from the Hay Cave fossil molluscan records via an analysis of shell sizes and whorl counts. These quantifications in turn can be linked to trends in relative frequency of land snail shells through the dated sequence. However, such comparisons also raise questions about the broader geographical applicability of existing palaeoenvironmental trends based on pollen.

The general shapes of the regression curves are likely to be reliable, given the stratified nature of the sequences which appear to possess good internal integrity. However, the degree of stretch (as opposed to the shape) of the regression curves — that is the length of each section of each curve — is dependent on the period of time covered rather than by the depth of deposits. Currently these curves have been presented by excavation unit, which basically represents depth below

ground. The last 3,100 years are over-emphasised in such curves, given peak sediment deposition rates during that time.

The early to mid Holocene period appears to be present in the Hay Cave sequence despite an absence of radiocarbon dates from this period, given the high land snail shell and CaCO_3 concretion frequencies from XU45 to XU34 (Figs 8,9). However, their exact timing is uncertain, given a total absence of radiocarbon determinations for this part of the

sequence.

The frequency of redeposited CaCO_3 can be taken as an indicator of changing moisture regimes, given the susceptibility of limestone to solution. The greater the solubility of a substance, the greater its liability to come out of solution. Many minerals are deposited in caves as chemical precipitates, and calcite is the mineral form of CaCO_3 . Although reactions are reversible, calcite is chiefly precipitated through the diffusion or 'degassing' of carbon dioxide (CO_2) from water into the atmosphere. To describe a general reaction, seepage water, initially enriched in CO_2 given the presence of soil and vegetation, becomes saturated in calcite when passing through joints in the limestone. Upon entering the cave environment with lower partial pressure of CO_2 in its atmosphere than in the soil above, CO_2 diffuses from dripping and flowing water and causes calcite to be precipitated out of solution and deposited. In essence, CaCO_3 deposition in caves implies a supply of water and vegetation growth sufficient to enrich soil water with carbon dioxide for limestone solution. From this, calcium carbonate is observed as an inorganic indicator of high moisture levels (Jennings, 1985)

The calcium carbonate curve is matched by other proxy indicators of environmental humidity. As a biological index, the incidence of land snail shell (Fig. 8) mimics the relative frequency of CaCO_3 concretions between 13,450 and 3,100 BP, an alliance related to the notion of Evans (1969) that essentially all molluscs are aquatic animals. As discussed, the habitats and behaviour patterns of terrestrial snails are largely controlled by the humidity of the environment. For example, *Hadra* aff. *bipartita*, a dominant taxon between XU45 and XU34, requires humid conditions. Observations on species in north

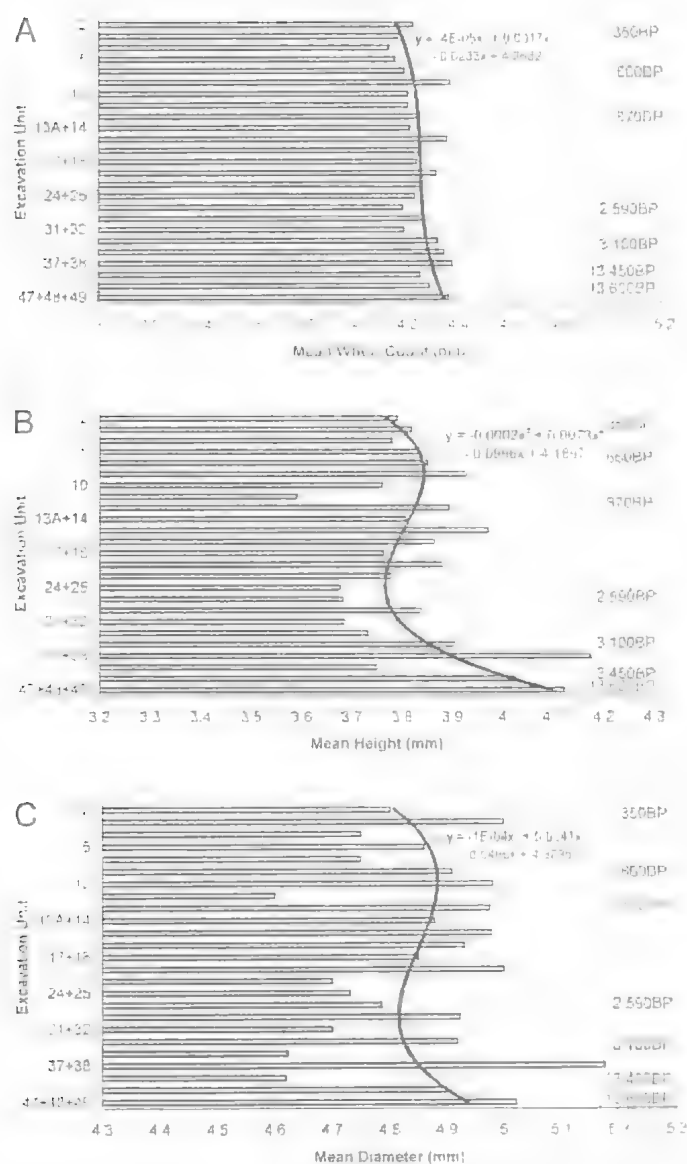


FIG. 10. *P. extincta* measurements by XL, Hay Cave. A, mean whorl count; B, mean height; C, mean diameter.

Queensland suggest that land snail activity is largely confined to the wet season, and hence there may be a relationship between the length of the wet season and number of individuals. The high shell accumulation, together with CaCO_3 concretions could indicate conditions were wettest during the period 13,450 to 3,100 BP in the Hay Cave sequence, independent of *P. extincta* shell measurements. This would be consistent with high rainfall regimes during the early to mid Holocene, as informed by existing

palaeoenvironmental data from other parts of north Queensland (see above).

It is difficult to determine why an absence of radiocarbon dates exists for the early to mid Holocene. The charcoal in the Hay Cave excavation is likely to all come from anthropogenic camp fires. As David & Lourandos (1997) recognised, however, there is no simple relationship between amount of charcoal in a site and the number of radiocarbon dates obtained. In turn, the number or presence of radiocarbon dates may not be indicative of the magnitude of human occupation, as biases in the creation, recovery, and preservation of charcoal and radiocarbon dates in a sequence or in a region are more likely to critically affect results. Biases may skew the date curve, and thus potentially falsify the common assumption that human occupation will produce more deposited carbon, even if the relationship is not strictly proportional. At Hay Cave this is well illustrated by the continued presence of burnt bone, shell and earth in the purported early Holocene levels where no radiocarbon dates have yet been obtained and charcoal is very sparse. We argue that such an absence of charcoal in these layers is not due to its original absence, as evident in the ample cases of burnt materials in those layers. Rather, charcoal has probably been removed post-depositionally, either as a result of high humidity levels rendering the charcoal fragile and susceptible to mechanical damage, or through other, as yet undetermined means.

This issue is currently the subject of further investigations by BD and HL.

However, increases in deposition rates of all cultural materials during the late Holocene indicate that broader factors are also at work. Land snail shell deposition rates, as calculated by numbers of *P. extincta* per unit time, show that shell frequencies were low within this early Holocene period, in comparison to the late Holocene. This may mean that terminal Pleistocene/early Holocene conditions were dry

rather than wet. If this was the case, this trend would question the validity of the above interpretations of CaCO_3 and total land snail concentrations as evidence of a wet phase. However, we would rather argue that the low frequency of *P. extincta* (and other small) shells during the early Holocene is due to their very small size and their inability to frequent soggy ground surface conditions, as was probably the case at the time (see above). If rainfall levels were significantly higher during the early to mid Holocene as it was during the terminal Pleistocene, which appears to be the case from the pollen evidence to the east, moisture regimes may have breached the upper thresholds for very small land snails (<6mm in size). This is consistent with the predominance of large species of shells at Hay Cave during this time, including the wet-adapted species *Hadra* aff. *bipartita*.

While the issue of continuous vs. intermittent deposition of sediments at Hay Cave is beyond the ability of this paper to resolve, its resolution may be important for a better understanding of palaeoenvironmental trends in the region as a whole. If in fact the sediment accumulation rate at Hay Cave is a function of the presence of Aboriginal people in the environment rather than of natural phenomena, compared to the late Holocene, the formation of only 27cm of deposit between $13,450 \pm 150$ and $3,100 \pm 60$ BP would be consistent with lower levels of human occupation than subsequently. For Hay Cave, what these late Holocene sediment increases mean in terms of human behaviour remains uncertain, but it is possible that, like Mitchell River Cave, Hearth Cave and Mordor Cave also in the Mitchell-Palmer region (David & Chant, 1995), intensive occupation did not begin until the late Holocene, and before this time the caves may not have been extensively used as living sites.

CONCLUSIONS

This paper has focused on techniques of land snail shell analysis and their usefulness to palaeoenvironmental reconstructions for the period spanning the Last Glacial Maximum to present in north Queensland. In the process, a wide range of themes have been covered, including: history of Aboriginal land use (archaeology); plant biogeography; geological and climatic processes; and land snail ecology and taxonomy, from historical as well as modern day perspectives.

It is salutary to recall here that the presence and value of molluscs in archaeological deposits was

recognised more than a century ago, and yet their detailed investigation has only recently begun in Australia. Considering the rapid development of palynology in the last 30 years, and together with the great potential of Mollusca to inform us on historical trends in both climatic and environmental change, it is perhaps rather surprising that such a state of affairs should have arisen (Evans, 1969). At present, nonetheless, most Australian studies of fossil land snails require taxonomic and ecological investigations of modern land snails to be undertaken before palaeoenvironmental research can be conducted. Once this necessity is accepted, a wealth of potential palaeoenvironmental information is available from fossil land snails. As is apparent from their abundance in buried deposits, their ability to be identified to species level, their sensitivity to moisture regimes, and their strong affinity with vegetation type, *P. extincta* snails have demonstrated their value as proxy indicators of palaeoenvironments in semi-arid landscapes. It is likely that both *P. extincta* and other species of land snails can be used for palaeoenvironmental research in other environmental zones in various parts of this continent.

An existing body of regional palaeoenvironmental evidence has provided a context for the Hay Cave land snail data. Although the quality of these data is variable, marked but variable community and taxon responses to glacial/interglacial cycling is apparent. The northeastern Queensland environment has been a dynamic and diverse system (or rather, interconnected set of systems) where the gross composition of the vegetation fluctuates in relation to cyclical changes in climate and sea level. The humid tropics region of northeastern Queensland has provided a substantial and detailed history of rainforest and rainforest-sclerophyll interactions via pollen analysis at a number of sites on the volcanic Atherton Tableland. These pollen sequences indicate that during the late Quaternary, the Tableland was subject to significant environmental variability. It has been proposed that similar changes in climate have been experienced throughout northern Queensland, although changes may not have been entirely synchronous nor of equal degree in all places.

Complementing these established palaeoenvironmental studies, we argue that *P. extincta* shell whorl counts are also dependent on moisture regimes and thus reflect fluctuations in

mean annual rainfall. Based largely on pollen research, last glacial maximum has been interpreted, independently of land snail research, as being a period of dry conditions. This was followed by a period of increased (to peak) precipitation during the early to mid Holocene. In its turn, this period of time was itself followed by an effective drying. These major changes in moisture regimes can be expected to have affected the spread, floristic structure and complexity of semi-deciduous vine thicket in north Queensland. Given *P. extincta*'s restricted distribution to such vegetational communities and their sensitivity to moisture, the broader applicability of our extant knowledge of palaeoenvironmental (including palaeoclimatic) trends can be tested and refined. Thus, the most important changes in the *P. extincta* record since 19,300 years BP are the relative increases in precipitation starting at 13,000 BP and a relative lack of whorl count variation at Hay Cave. Results at Hay Cave, to some degree, differ from those of the Atherton Tableland models based on pollen analyses, which have so far largely failed to address their relevance for regions to the west of the Great Divide. Far from constituting negative evidence, in contrast to the Atherton curves, the Hay Cave data suggests a more stable rainfall regime through time, although directions of change are consistent with the Atherton trends. As Head & Stuart (1980) concluded, this type of pattern has the potential to help quantify the limits within which climate systems operate.

The lower magnitude of environmental change west of the Great Dividing Range suggested by this study now warrants further investigation. Given the current status of land snail research, multidisciplinary studies would aid in assessing the extent of this phenomenon, as well as testing the accuracy of land snail models in palaeoenvironmental reconstructions. The need for the application of additional tests in such research was briefly demonstrated in this paper by a consideration of the formation of CaCO_3 concretions in cave sediments, and of depositional frequencies of all land snail species. A more extensive investigation of these issues may provide a better impression of past moisture levels and palaeoenvironmental factors than a consideration of *P. extincta* alone has been able to. Further insights into the ecology of other land snail species may also enhance our ability to model palaeoenvironments via excavated fossil land snail shells.

Although good long-term data from ecological and biological information is available on *P. extincta* shells, there is still a need to refine our understanding of this species. In particular, *P. extincta* deposition rates before and after 3,100 BP raise more questions than answered here; further sediment analyses may clarify some of these questions. Similarly, the changes in *P. extincta* shell characteristics documented here may indicate changes in human and climatic impacts on sedimentation rates within caves. Further attempts should be made to determine the influence of human activities on ecosystems within the Mitchell-Palmer region, and how people may have adjusted to environmental change in the past.

In recognising the ability of vegetation to accommodate to changes in certain environmental variables, it is probable that the Chillagoe Formation vine thickets are now remnants of a more extensive Pleistocene-early Holocene flora, now represented as permanent refugia. In this sense, *P. extincta* highlights the relevance of, and promotes the need for, knowledge of scales of biotic changes in the recent past and for 'dynamic' conservation strategies to accommodate these.

In short, the main value of this work is that the land snail data point to a reasonable but limited degree of variability in palaeoenvironmental change for hitherto unstudied parts of north Queensland. In particular, it questions the exact applicability of the Atherton curves to inland regions, while at the same time supporting established trend directions. The use of *P. extincta* in this project indicates that land snails represent a significant and new potential source of data for Australian palaeoecological studies.

ACKNOWLEDGEMENTS

We thank Kylie Stumkat for SEM work; the Queensland Museum for photography and for a Summer Scholarship for CR; Monash University for a Logan Fellowship to BD; Gary Swinton of the Department of Geography and Environmental Science, Monash University, for Figure 1; Lana Little for assistance with fieldwork, data collection and for comments on an earlier draft of this paper; Prof. Peter Kershaw for comments on aspects of this work; Chris Clarkson for helping with the Hay Cave excavation; Earthwatch and the 1996 Earthcorps for helping with all aspects of the fieldwork; Angela Holden for sorting much of the Hay Cave material; AINSE for a radiocarbon grant to HL; Ewan Lawson and

ANSTO's ANTARES AMS laboratory for undertaking the radiocarbon dates; and Mrs Ethel Ahlers for kindly supplying the rainfall data for Bellevue Station.

LITERATURE CITED

- AHARON, P. 1983. Surface ocean temperature variations during the late Wisconsin stage: $^{16}\text{O}/^{18}\text{O}$ isotopic evidence from Papua New Guinea. Pp. 3-4. In Chappell, J. & Grindrod, J. (eds) CLIMANZ: Proceedings of First CLIMANZ, February 1981, Dept. Biogeography and Geomorphology, R.S.Pac.S. (Australian National University: Canberra).
- ALLEN, M.J. 1991. Analysing the landscape: a geographical approach to archaeological problems. Pp. 37-54. In Schofield, A.J. (ed.) Interpreting artefact scatters: contributions to ploughzone archaeology. (Oxbow Books: Oxford).
1992. Environment and landuse: the economic development of the community who built Stonehenge (an economy to support the stones). Proceedings of the British Academy 92: 115-144.
1994. The land-use history of the southern English Chalklands with an evaluation of the Beaker Period using environmental data: colluvial deposits as environmental and cultural indicators. Unpubl. PhD thesis, University of Southampton, Southampton.
- 1995a. Land molluscs. Pp. 92-100. In Wainwright, G.J. & Davies, S.M. (eds) Barksbury Camp, Hampshire: excavations 1973 and 1981. English Heritage Archaeological Report 4. (English Heritage: London).
- 1995b. The prehistoric land-use and human ecology of the Malling-Caburn Downs: two late Neolithic/Early Bronze Age sites beneath colluvium. Sussex Archaeological Collections 133: 19-43.
1997. Environment and land-use: the economic development of the communities who built Stonehenge (an economy to support stones). Pp. 115-144. In Cunliffe, B.W. & Renfrew, A.C. (eds) Science and Stonehenge. Proceedings of the British Academy 92.
- In press. High resolution mapping in Neolithic and Bronze Age landscapes and land-use: the combination of multiple palaeo-environmental analysis and topographic modelling. In Fairbairn, A. (ed.) Landscape and environment, economy and society: plants in Neolithic Britain. (Oxbow Books: Oxford).
- ALLEN, M.J., MORRIS, M. & CLARK, R.H. 1995. Food for the living: a reassessment of a Bronze Age barrow at Bucksdon, Basingstoke, Hampshire. Proceedings of the Prehistoric Society 61: 157-189.
- ALLEN, M.J. & WYLES, S. 1993. The landuse history: the molluscan evidence. Pp. 45-50. In Graham, A. & Newman, C. (eds) Recent excavations of Iron Age and Romano-British enclosures in the Avon Valley, Wiltshire. Wiltshire Archaeology and Natural History Magazine 86: 8-57.
- BELL, F.C., WINTER, J.W., PAHL, L.I. & ANDERSON, R.G. 1987. Distribution, area and tenure of rainforest in northeastern Australia. Proceedings of the Royal Society of Queensland 98: 27-39.
- BENGSTON, S.A., NILSSON, A., NORDSTROM, S. & RUNDGREN, S. 1979. Selection for adult shell size in natural populations of the landsnail *Cepaea hortensis* (Muller). Annales Zoologici Fennici 16: 187-194.
- BISHOP, M.J. 1981. The biogeography and evolution of Australian land snails. Pp. 924-954. In Keast, A. (ed.) Ecological biogeography of Australia. (Dr W. Junk: The Hague).
- BOWLER, J. 1983. 18±2KA: northern Australia hydrologic evidence. Pp. 47-48. In Chappell, J. & Grindrod, J. (eds) CLIMANZ: Proceedings of First CLIMANZ, February 1981. Dept. Biogeography and Geomorphology, R.S.Pac.S. (Australian National University: Canberra).
- BUTLER, D. 1998. Environmental change in the Quaternary. Pp. 78-97. In David, B. (ed.) Ngarrabullgan: geographical investigations in Djungan Country, Cape York Peninsula, Monash Publications in Geography and Environmental Science 51. (Monash University: Clayton).
- CARNAHAN, J.A. 1989. Australia: present vegetation (map). (Australian Surveying and Land Information Group, Dept. of Administrative Services: Canberra).
- CARTER, S.P. 1990. The stratification and taphonomy of shells in calcareous soils: implications for land snail analysis in archaeology. Journal of Archaeological Science 17: 495-508.
- CHAPPELL, J. 1982. Sea levels and sediments: some features of the context of coastal archaeological sites in the tropics. Archaeology in Oceania 17: 69-78.
- CHAPPELL, J., CHIVAS, A., WALLENSKY, E., POLACH, H. & AHARON, P. 1983. Holocene palaeoenvironmental changes, central to north Great Barrier Reef inner zone. Bureau of Mineral Resources Journal of Geology and Geophysics 8: 223-235.
- CHILLAGOE CAVING CLUB 1982. Chillagoe karst: a speleological field guide to the towers and caves of the Chillagoe-Mungana-Rookwood areas in Far North Queensland, Australia. (Chillagoe Caving Club: Cairns).
1988. Mitchell-Palmer karst: a speleological field guide for the towers and caves of the Mitchell-Palmer areas in Far North Queensland, Australia. (Chillagoe Caving Club: Cairns).
1990. Chillagoe karst: a speleological field guide to the towers and caves of the Chillagoe-Mungana-Rookwood areas in Far North Queensland, Australia. Supplement Number 2 (Chillagoe Caving Club: Cairns).

- CLEAL, R.M.J. & ALLEN, M.J. 1994. Investigation of tree-damaged barrows on King Barrow Ridge and Luxenborough Plantation, Amesbury. Wiltshire Archaeological and Natural History Magazine 87: 54-84.
- CONNAH, G. & McMILLAN, N.F. 1964. Snails and archaeology. *Antiquity* 38: 62-64.
- DAVID, B. & CHANT, D. 1995. Rock Art and regionalisation in North Queensland prehistory. *Memoirs of the Queensland Museum* 37: 357-528.
- DAVID, B. & LOURANDOS, H. 1997. 37,000 years and more in tropical Australia: investigating long-term archaeological trends in Cape York Peninsula. *Proceedings of the Prehistoric Society* 63: 1-23.
- DAVID, B. & STANISIC, J. 1991. Land snails in Australian archaeology: initial results from Echidna's Rest (north Queensland). *The Artefact* 14: 19-24.
- EVANS, J.G. 1969. Land and freshwater Mollusca in archaeology: chronological aspects. *World Archaeology* 1: 170-183.
- 1971a. Habitat change on the calcareous solid of Britain: the impact of Neolithic man. Pp. 27-73. In Simpson, D.D.A. (ed.) *Economy and settlement in Neolithic and early Bronze Age Britain and Europe*. (Leicester University Press: Leicester).
- 1971b. Notes on the environment of early farming communities in Britain. Pp. 11-26. In Simpson, D.D.A. (ed.) *Economy and settlement in Neolithic and early Bronze Age Britain and Europe*. (Leicester University Press: Leicester).
1972. Land snails in archaeology. (Seminar Press: London).
- FENSHAM, R.J. 1995. Floristics and environmental relations of inland dry rainforests in north Queensland, Australia. *Journal of Biogeography* 22: 1047-1063.
1996. Land clearance and conservation of inland dry rainforest in north Queensland, Australia. *Biological Conservation* 75: 289-298.
- GALLOWAY, R.W. & KEMP, E.M. 1981. Late Cainozoic environments in Australia. Pp. 52-80. In Keast, A. (ed.) *Ecological biogeography of Australia*. (Dr W. Junk: The Hague).
- GALLOWAY, R.W., GUNN, R.H. & STONY, R. 1970. Lands of the Mitchell-Normanby Area. CSIRO Land Research Series 26. (CSIRO: Canberra).
- GILLISON, A.N. 1987. The dry rainforests of Terra Australis. Pp. 305-321. In Werren, G. & Kershaw, A.P. (eds) *The Rainforest Legacy: Australian National Rainforest Survey*, Vol. 1. (Australian Government Publishing Service: Canberra).
- GOODFRIEND, G.A. 1986. Variation in land-snail shell form and size and its causes: a review. *Systematic Zoology* 35: 204-223.
1992. The use of land snails in palaeoenvironmental reconstruction. *Quaternary Science Reviews* 11: 665-685.
- GOULD, S.J. 1984. Covariance sets and ordered geographic variation in *Cerion* from Aruba, Bonaire and Curacao: a way of studying nonadaptation. *Systematic Zoology* 33: 217-237.
- HEAD, L. & STUART, I.M.F. 1980. Change in the Aire: Palaeoecology and prehistory in the Aire Basin, southwestern Victoria. *Monash Publications in Geography* 24. (Monash University: Clayton).
- HISCOCK, P. 1984. Preliminary report on the stone artefacts from Colless Creek Cave, northwestern Queensland. *Queensland Archaeological Research* 1: 120-151.
- HISCOCK, P. & KERSHAW, A.P. 1992. Palaeoenvironments and prehistory of Australia's tropical Top End. Pp. 43-75. In Dodson, J. (ed.) *The Naive Lands: Prehistory and environmental change in Australia and the southwest Pacific*. (Longman Cheshire: Melbourne).
- HOPKINS, M.S., ASH, J., GRAHAM, A.W., HEAD, J. & HEWETT, R.K. 1993. Charcoal evidence of the spatial extent of the *Eucalyptus* woodland expansions and rainforest contractions in north Queensland. *Journal of Biogeography* 20: 357-372.
- HOPLEY, D. 1983. Evidence of 15,000 years of sea level change in tropical Queensland. Pp. 93-104. In Hopley, D. (ed.) *Australian sea levels in the last 15,000 years: a review*. Occasional Paper 3. (Dept. of Geography, James Cook University of North Queensland: Townsville).
- HUGHES, P. 1983. Colless Creek rockshelter archaeological site, NW Queensland, 18KA. Pp. 59-61. In Chappell, J. & Grindrod, J. (eds) *CLIMANZ: Proceedings of First CLIMANZ*, February 1981. Dept. Biogeography and Geomorphology, R.S.Pac.S. (Australian National University: Canberra).
- IREDALE, T. 1937. A basic list of the land Mollusca of Australia. Part II. *Australian Zoologist* 9: 1-39.
1938. A basic list of land Mollusca of Australia. Part III. *Australian Zoologist* 9: 83-124.
- JENNINGS, J.N. 1985. *Karst geomorphology*. (Basil Blackwell: Oxford).
- KAHN, T.P. & LAWRIE, B.C. 1987. Vine thickets of the inland Townsville region. Pp. 159-201. In Werren, G. & Kershaw, A.P. (eds) *The Rainforest Legacy: Australian National Rainforest Survey*, Vol. 1. (Australian Government Publishing Service: Canberra).
- KEMP, E.M. 1981. Tertiary Palaeogeography and the evolution of the Australian climate. Pp. 32-49. In Keast, A. (ed.) *Ecological biogeography of Australia*. (Dr W. Junk: The Hague).
- KENNARD, A.S. 1897. The post Pliocene non-marine Mollusca of Essex. *Essex Nature* 10: 87-109.
- KERSHAW, A.P. 1970. A pollen diagram from Lake Euramoo, north-east Queensland, Australia. *New Phytologist* 69: 785-805.

1971. A pollen diagram from Quincan Crater, north-east Queensland, Australia. *New Phytolith* 70: 669-681.
1974. A long continuous pollen sequence from north-eastern Australia. *Nature* 251: 222-223.
1975. Late Quaternary vegetation and climate in north-eastern Australia. Pp. 181-187. In Suggate, R.P. & Creswell, M.M. (eds) *Quaternary Studies*. (Royal Society of New Zealand: Wellington).
1976. A late Pleistocene and Holocene pollen diagram from Lynch's Crater, north-eastern Queensland, Australia. *New Phytolith* 77: 469-498.
1985. An extended late Quaternary vegetation record from north-eastern Queensland and its implications for the seasonal tropics of Australia. *Proceedings of the Ecological Society of Australia* 13: 179-189.
1986. Climatic change and Aboriginal burning in north-east Australia during the last two glacial/interglacial cycles. *Nature* 322: 47-49.
1994. Pleistocene vegetation of the humid tropics of northeastern Queensland, Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 109: 339-412.
- KERSHAW, A.P., MCKENZIE, G.M. & McMINN, A. 1993. A Quaternary vegetation history of northeastern Queensland from pollen analysis of ODP site 820. In McKenzie, J.A., Davie, P.J. & Palmer-Johnson, A. (eds) *Proceedings of the Ocean Drilling Program, Scientific Results* 133: 107-114.
- KERSHAW, A.P., QUILTY, P.G., DAVID, B., VAN HUET, S. & McMINN, A. 2000. *Palaeobiogeography of the Quaternary of Australasia*. *Memoir of the Association of Australasian Palaeontologists* 23: 471-516.
- LAMB, L. 1996. Investigating changing stone technologies, site use and occupational intensities at Fern Cave, north Queensland. *Australian Archaeology* 42: 1-7.
- LEES, B.G., YU, Y. & PRICE, D.M. 1992. Thermoluminescence dating of dunes at Cape St. Lambert, East Kimberley, northern Australia. *Marine Geology* 106: 131-139.
- LOWE, J.J. & WALKER, M.J.C. 1984. *Reconstructing Quaternary environments*. (Longman: London).
- MCGLONE, M.S., KERSHAW, A.P. & MARKGRAF, V. 1992. El Nino/Southern Oscillation climatic variability in Australasian and South American palaeoenvironmental records. Pp. 435-462. In Diaz, H.F. & Markgraf, V. (eds) *El Nino: historical and palaeoclimatic aspects of Southern Oscillation*. (Cambridge University Press: Cambridge).
- NIX, A. & KALMA, J.D. 1972. Climate as a dominant control in the biogeography of northern Australia and New Guinea. Pp. 61-92. In Walker, D. (ed.) *Bridge and barrier: the natural and cultural history of Torres Strait*, pp. Dept. Biogeography and Geomorphology, R.S.Pac.S. (Australian National University: Canberra).
- O'CONNER, T. 1988. Slums, puddles and ditches: are molluscs useful indicators. Pp. 61-68. In Murphy, P. & French, C. (eds) *The exploration of wetlands*. (British Archaeological Reports 186: Oxford).
- ODHNER, N. 1917. Results of Dr E Mjöberg's Swedish Scientific Expeditions to Australia 1910-1913. XVII. Mollusca. *Kungliga Svenska Vetenskapsakademiens Handlingar* 52: 1-115.
- OWEN, D.T. 1965. A population study of an equatorial land snail, *Limnicolaria martensiana* Achatinidae). *Proceedings of the Zoological Society of London* 144: 361-382.
- POKRYSZKO, B.M. 1996. The Gastrocoptinae of Australia (Gastropoda: Pulmonata: Pupilloidea): Systematics, distribution, and origin. *Invertebrate Taxonomy* 10: 1085-1150.
- PORCH, N. In press. Palaeoenvironmental interpretation of late Quaternary non-marine mollusc assemblages from Pulbeena Swamp, northwestern Tasmania. *Alcheringa*.
- PORCH, N. & ALLEN, J. IN PREP. A 35,000 year land snail and vertebrate sequence from Wareen Cave, a late Pleistocene archaeological site in southwest Tasmania. To be submitted to *Journal of Archaeological Science*.
- ROBINSON, T.W.L. 1982. Limestone solution experiment at Chillagoe. *Tower Karst* 4: 71-76.
- ROBINSON, M. 1988. Molluscan evidence for pasture and meadowland on the floodplain of the upper Thames basin. Pp. 101-112. In Murphy, P. & French, C. (eds) *The exploitation of the wetlands*. (British Archaeological Reports, British Series 186: Oxford).
- SCAIFE, R.G. 1995. Boreal and Sub-boreal chalk landscape: pollen evidence. Pp. 51-55. In Cleal, R.M.J., Walker, K.E. & Montague, R. (eds) *Stonehenge in its landscape: the twentieth century excavations*. (English Heritage Archaeological Report 10: London).
- SHARPLES, N.M. 1991. Maiden Castle: excavations and field survey 1985-6. (English Heritage Archaeological Report 19: London).
- SHULMEISTER, J. & LEES, B.G. 1995. Pollen evidence from tropical Australia for the onset of an ENSO dominated climate at c.4000 BP. *The Holocene* 5(1): 10-18.
- SINGH, G., KERSHAW, A.P. & CLARK, R. 1981. Quaternary vegetation and fire history in Australia. Pp. 23-54. In Gill, A.M., Groves, R.H. & Noble, I.R. (eds) *Fire and the Australian biota*. (Australian Academy of Science: Canberra).
- SMITH, B.J. 1992. Non-marine Mollusca. Pp. 1-405. In Houston, W.W.K. (ed.) *Zoological Catalogue of Australia*. Australian Government Publishing Service: Canberra).
- SMITH, B.J. & KERSHAW, R.C. 1979. *Field guide to the non-marine molluscs of South Eastern*

- Australia. (Australian National University Press: Canberra).
1981. Tasmanian land and freshwater molluscs. Fauna of Tasmania Handbook Series, No. 5. (University of Tasmania: Hobart).
- SMITH, B.J. & STANISIC, J. 1998. Pulmonata: Introduction. Pp. 1037-1061. In Beesley, P.L., Ross, G.J.B. & Wells, A. (eds) Mollusca: the southern synthesis. Fauna of Australia 5B. (CSIRO Publishing: Melbourne).
- SOLEM, A. 1972. Mollusks from prehistoric sites in Afghanistan. Transactions of the American Philosophical Society 62: 57-65.
1974. The shell makers: introducing Mollusks. (John Wiley & Sons: New York).
1976. Endodontoid land snails from Pacific Islands. Part I. Family Endodontidae. Fieldiana: Zoology, Special Publication pp. 1-508.
1982. Small land snails from northern Australia. II. Species of *Westracystis* Iredale, 1939 (Mollusca: Pulmonata, Helicarionidae). Journal of the Malacological Society of Australia 5: 175-193.
1984. Small land snails from Northern Australia. III: Species of Helicodiscidae and Charopidae. Journal of the Malacological Society of Australia 6: 155-179.
1988. Maximum in the minimum: biogeography of land snails from the Ningbing Ranges and Jeremiah Hills, north-east Kimberley, Western Australia. Journal of the Malacological Society of Australia 9: 59-113.
1991. Land snails of the Kimberley rainforest patches and biogeography of all Kimberley land snails. Pp. 145-246. In McKenzie, N.L., Johnston, R.B. & Kendrick, P.G. (eds) Kimberley rainforests of Australia. (Surrey Beatty & Sons: Chipping Norton).
- 1992a. Camaenid land snails from southern and eastern South Australia, excluding Kangaroo Island. Part 1. Systematics, distribution and variation. Records of the South Australian Museum, Monograph Series 2: 1-338.
- 1992b. Camaenid land snails from southern and eastern South Australia, excluding Kangaroo Island. Part 2. Biogeography and covariation. Records of the South Australian Museum, Monograph Series 2: 339-424.
- SOLEM, A. & CHRISTENSEN, C.C. 1984. Camaenid land snail reproductive cycle and growth patterns in semiarid areas of north-western Australia. Australian Journal of Zoology 32: 471-491.
- SPARKS, B.W. 1969. Non-marine Mollusca and archaeology. Pp. 395-406. In Brothwell, D. & Higgs, E. (eds) Science in Archaeology. (Thames & Hudson: London).
- STANISIC, J. 1990. Systematics and biogeography of eastern Australian Charopidae (Mollusca, Pulmonata) from subtropical rainforests. Memoirs of the Queensland Museum 30(1): 1-238.
- 1994a. The distribution and patterns of species diversity of land snails in eastern Australia. Memoirs of the Queensland Museum 36(1): 207-214.
- 1994b. Landsnails of the Wet Tropics biogeographic region, northeastern Queensland. Australian Shell News 87 (October): 1-2.
- 1997a. Land snail diversity in Queensland: an overview. Part 1. Australasian Shell News 94: 6.
- 1997b. Land snail diversity in Queensland: an overview. Part 2. Australasian Shell News 95: 6.
- 1997c. An area of exceptional land snail diversity: the Macleay Valley, northeastern New South Wales. Memoirs of the Museum of Victoria 56: 441-448.
- 1997d. Land snails of the Chillagoe limestones. Australasian Shell News 96: 3-6.
1998. A survey of the land snails of the land snails of the Queensland Brigalow Lands: Their distribution, conservation status and close association with vine thickets. Unpublished report to the Queensland Department of Environment (Queensland Museum: Brisbane).
1999. Land snails and dry vine thickets in Queensland: using museum invertebrate collections in conservation. Pp. 257-263. In Ponder, W. & Lunney, D. (eds) The other 99%. The conservation and biodiversity of invertebrates. Transactions of the Royal Zoological Society of New South Wales. (Surrey Beatty & Sons: Chipping Norton).
- STANISIC, J. & INGRAM, G.J. 1998. Sandstone, snails and slaters: Pp. 112-118. In David, B. (ed.) Ngarrabullgan: geographical investigations in Djungan Country, Cape York Peninsula' Monash Publications in Geography and Environmental Science, Number 51. (Monash University: Melbourne).
- STANISIC, J., EDDIE, C., HILL, A. & POTTER, D. 1994. A preliminary report on the distribution of land snails occurring within the Wet Tropics area. Unpubl. report to the Wet Tropics Management Authority. (Queensland Museum: Brisbane).
- STEPHANS, K. & L. HEAD, L. 1995. Palaeoecology of archaeological and swamp sites in SE Cape York Peninsula. Pp. 18-32. In Morwood, M. & Hobbs, D.R. (eds) Quinkan prehistory: the archaeology of Aboriginal art in southeast Cape York Peninsula, Australia. (Tempus 3. University of Queensland: St. Lucia).
- TILLIER, S. 1981. Clines, convergence and character displacement in New Caledonian diplommatinids (land prosobranchs). Malacologia 21: 177-208.
- TORGENSEN, T., LULY, J., DE DECKKER, P., JONES, M.R., SEARLE, D.E., CHIVAS, A.R. & ULLMAN, W.J. 1988. Late Quaternary environments of the Carpentaria Basin, Australia. Palaeogeography, Palaeoclimatology, Palaeoecology 67: 245-261.
- WAINWRIGHT, G.J. & DAVIES, S.M. 1995. Balksbury Camp, Hampshire: Excavations 1973

- and 1981. English Heritage Archaeological Report 4. (English Heritage: London).
- WEBB, L.J. & TRACEY, J.G. 1981. Australian rainforests: patterns and change. Pp. 605-694. In A. Keast, A. (ed.) Ecological biogeography of Australia. (Dr W. Junk: The Hague).
- WINTER, J.W., BELL, F.C., PAHL, L.L. & ATHERTON, R.G. 1987. The distribution of rainforest in north-eastern Queensland. Pp 223-227. In Werren, G. & Kershaw, A.P. (eds) The Rainforest Legacy: Australian National Rainforest Survey, Vol. 1. (Australian Government Publishing Service: Canberra).
- WOODWARD, B.B. 1908. Notes on the drift and underlying deposits at Newquay, Cornwall. Geology Magazine V (5): 10-18, 80-87.

APPENDIX 1

Locality data for *P. extincta* from Mitchell-Palmer area. (QM reg. no., locality and habitat data, latitude/longitude).

- MO22998, Laura-Palmerville Rd, N of Palmerville, 15°48'45"S, 144°03'46"E
- MO23375, Laura-Palmerville Rd, N of Palmerville, 15°53'20"S, 144°05'20"E
- MO61172, Limestone Ck Rd, SSE of Palmerville, 16°02'36"S, 144°07'32"E
- MO61191, Limestone Ck Rd, SSE of Palmerville, 16°02'51"S, 144°08'28"E
- MO23592, Limestone Ck Rd, SSE of Palmerville, 16°02'53"S, 144°07'23"E
- MO61205, Limestone Ck Rd, SSE of Palmerville, 16°03'13"S, 144°08'24"E
- MO61156, Limestone Ck Rd, SSE of Palmerville, 16°03'22"S, 144°07'39"E
- MO23584, Limestone Ck Rd, SSE of Palmerville, 16°07'33"S, 144°08'47"E
- MO23388, Limestone Ck Rd, SSE of Palmerville, 16°08'58"S, 144°09'07"E

Locality data for *P. extincta* from Chillagoe-Mungana area. (QM reg. no., locality and habitat data, latitude/longitude).

- MO15955, Marachoo Cave, 17°05'39"S, 144°23'28"E
- MO25996, Carpentaria Cave, 17°05'46"S, 144°23'56"E
- MO50231, Capricorn Cave, 17°06'15"S, 144°24'36"E
- MO53325, Chillagoe, c.13km WNW on Chillagoe-Mungana Rd, 17°06'15"S, 144°23'40"E
- MO58485, Chillagoe, c.10km WNW on Chillagoe-Mungana Rd, 17°06'45"S, 144°24'55"E
- MO53335, Chillagoe, c.10km WNW on Chillagoe-Mungana Rd, 17°06'45"S, 144°24'55"E
- MO53551, Chillagoe, c.3km N on road to Metal Hills, 17°07'20"S, 144°31'10"E
- MO19527, Spring Cave, 17°08'03"S, 144°25'30"E
- MO50229, Tea Tree Cave, 17°10'33"S, 144°08'18"E
- MO53448, Chillagoe, c.3km SW on road to Royal Arch Caves, 17°10'35"S, 144°00'15"E
- MO58540, Chillagoe, c.3km SW on road to Royal Arch Caves, 17°10'35"S, 144°00'15"E
- MO53436, Chillagoe, c.6km SW at Royal Arch Caves, 17°11'15"S, 144°30'00"E
- MO38499, Chillagoe, c.8km SE on road to Almaden, 17°11'20"S, 144°33'05"E
- MO53564, Chillagoe, c.8km SE on road to Almaden, 17°11'20"S, 144°33'05"E
- MO58547, Chillagoe, c.8km SE on road to Almaden, 17°11'20"S, 144°33'05"E

OBSERVATIONS ON THE POSTCRANIAL MORPHOLOGY, ONTOGENY AND
PALAEOBIOLOGY OF *SCLEROCEPHALUS HAEUSERI* (AMPHIBIA:
ACTINODONTIDAE) FROM THE LOWER PERMIAN OF SOUTHWEST GERMANY

ULLA LOHMANN AND SVEN SACHS

Lohmann, U. & Sachs, S. 2001 06 30: Observations on the postcranial morphology, ontogeny and palaeobiology of *Sclerocephalus haeuseri* (Amphibia: Actinodontidae) from the Lower Permian of Southwest Germany. *Memoirs of the Queensland Museum* 46(2): 771-781, Brisbane. ISSN 0079-8835.

The temnospondyl amphibian *Sclerocephalus*, in particular its postcranial anatomy, is described in 4 ontogenetic stages: larval, juvenile, adult and late adult. Some specimens preserve stomach contents, consisting of paramblypterid fishes and small amphibians (*Micromelerpeton*, *Apateon*). In one specimen, the remains of a small *Sclerocephalus* were found. Larval and juvenile individuals probably lived in a different habitat than adult and late adult ones. In the juvenile, adult and late adult stages, *Sclerocephalus* was the top predator in its environment. □ *Amphibia*, *Limnarchia*, *Actinodontidae*, *Sclerocephalus haeuseri* postcranial morphology, ontogeny, Lower Permian, Germany.

Ulla Lohmann, Institute of Tropical Environmental Studies and Geography, James Cook University, Townsville 4811, (e-mail: ulla@ullalohmann.de); Sven Sachs, Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; 28 March 2001.

Sclerocephalus is one of the best-known limnarchian amphibians in the Lower Permian of Central Europe. The type species, *S. haeuseri*, was described by Goldfuss (1847), but the holotype is lost (Boy, 1988). *Sclerocephalus* was described or referred to by several researchers (Ammon, 1889; Boy, 1976, 1988; Branco, 1887; Broili, 1908, 1926; Burmeister, 1850; Credner, 1893; Fritsch, 1901; Heyler, 1975; Meyer, 1857, 1858; Romer, 1947; Werneburg, 1983, 1989, 1992). Three known species are: *S. haeuseri* Goldfuss, 1847, *S. bavaricus* Branco, 1887 and *S. jogischneideri* Werneburg, 1992. Other species referred to *Sclerocephalus* do not belong to that taxon, e.g. '*S. latirostris* Jordan, 1849 (= *Cheliderpeton latirostre* sensu Boy, 1993), '*S. labyrinthicus* Geinitz, 1861 (= *Onchiodon labyrinthicus* sensu e.g. Watson, 1919) and '*S. credneri* Fritsch, 1901 (= *Onchiodon labyrinthicus* sensu Werneburg, 1993 and *Capetus palustris* sensu Sequeira & Milner, 1993). On the other hand some larval individuals of *Sclerocephalus* were first misinterpreted and therefore described as or referred to other taxa. Romer (1939) first pointed out that *Branchiosaurus anblystomus* described by Credner (1882, 1885, 1886, 1893) and Ammon (1889) belonged to *Sclerocephalus* (Credner's specimens are today assigned to *Onchiodon* (sensu Boy, 1990)). Later Boy (1972) recognised that *Leptorophus levis* Bulman, 1928 (= *Branchiosaurus levis* in Watson, 1963) and

Pelosaurus longiscutatus Theobald, 1958 may represent larval individuals of *Sclerocephalus*.

Sclerocephalus had a wide palaeogeographical distribution (Werneburg, 1988) and is recorded throughout the Autunian. The oldest known species is *S. bavaricus* from the Altenglan Formation (Lower Autunian) of Ohmbach (Rheinland Pfalz, SW Germany). It is represented by only one incomplete skeleton (MB Am.442) with a well-preserved skull.

The type species *S. haeuseri* is best known and is represented by a large number of articulated skeletons, from the Saar-Nahe area in SW Germany (Rheinland Pfalz and the Saarland). Two subspecies were recognised by Boy (1988): *S. h. haeuseri* Goldfuss, 1847 and *S. h. jeckenbachensis* Boy, 1988. It is also the only species for which all ontogenetic stages are known.

New specimens, showing different ontogenetic stages, have been found during the last decade. They also provide new data concerning diet. This paper characterises the stages of ontogeny of *S. haeuseri* and discusses its autecology.

MATERIAL AND METHODS

MATERIAL. PMNB uncataloged, PMNB 393, larval individuals, complete skeleton with soft tissue preservation, length 8.5 and 9.5 cm; GMS 307, larval individual, skull and pectoral girdle, skull length 16 mm; PMNB 85, juvenile, complete skeleton with soft tissue preservation, length 13 cm; PMNB 308, 177 juveniles, complete

skeleton with soft tissue preservation, length 11 and 12.5cm; PMNB 179, juvenile, skull and parts of the pectoral girdle, skull length 18mm; GMS 24, juvenile, skull and parts of the pectoral girdle, skull length 25mm; GMS 228, 395, juveniles, complete skeleton with soft tissue preservation, length 14 and 24cm; GMS 394, juvenile, skull and anterior half of the body with soft tissue preservation, skull length 35mm; GMS 52, juvenile, complete skeleton with soft tissue preservation, length 30cm; PMNB 174, juvenile, almost complete skeleton with soft tissue preservation, length 22cm; GMS 396, PMNB 93, juvenile, complete skeleton with soft tissue preservation, length 26cm; PMNB 103, GMS 348, PMNB 415, GMS 226, PMNB GRE-1, juveniles, complete skeleton with soft tissue preservation, length 25, 28, 29, 30, 48cm, respectively; PMNB uncatalogued, juvenile, complete skeleton with soft tissue preservation, length 26cm; PMNB PDC 327, adult, complete skeleton, length 74cm; PMNB BGC 69, adult, complete skeleton, length 72cm; PMNB BGC 112, adult, complete skeleton, length 79cm; BSPHG-1981 199, adult, skull and partial skeleton, skull length 16cm, PMNB BGC 112, late adult, complete skeleton, length 182cm. GMS P/70, adult, isolated pelvis, length ca. 10cm. Private collection SKO, adult, complete skeleton, length 82cm.

REFERRED MATERIAL. About 800 coprolites from PMNB, GMS, GPIM and SKO.

LOCALITIES AND AGE. All larval and most of the juvenile specimens are from Rümmelbach/Gresaubach (Top L-O 10). One juvenile is from Gresaubach (PMNB GRE-1, Top L-O 10) and one from Wörsbach (PMNB uncatalogued, Top L-O 10). Adults are from Niederhausen an der Appel (PMNB PDC 327, L-O 8), Jeckenbach (PMNB BGC 69, L-O 6), Odernheim (SKO uncatalogued, L-O 6) and Raumbach (SKO no Nr., L-O 6). The oldest adult was found in Jeckenbach (PMNB BGC 112, L-O 6). The isolated pelvis was found in St. Wendel (GMS P/70, L-O 5). The coprolites are from horizons Q 1 to L-O 10. In general the collecting horizons are in the Lower Rotliegendes (Autunian of European stratigraphy sensu Boy & Fichter or Gzhelian/Asselian in global stratigraphy sensu Deitze, 2000).

METHODS. All specimens were drawn proportionally from radiographs. For smaller individuals a WILD M-3 binocular with camera lucida was used.

REPOSITORIES. BSPHG, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich; PMNB, Pfalzmuseum für Naturkunde, Bad Dürkheim; GMS, Geologisches Museum der Saarberge AG, Saarbrücken; GPIM, Geologisch-Paläontologisches Institut, University of Mainz; MB, Museum für Naturkunde, Berlin; SKO, private collection Krätschmer, Odernheim.

ABBREVIATIONS. *Geological.* L-O, Lauterecken-Odernheim-Formation (current stratigraphy Lauterecken-Formation L-O 1 + L-O 2, Jeckenbach-Odernheim-Formation L-O 3 – L-O 10 (3 = lowermost/10 = uppermost). Q Quimbach-Formation (Q1 = lower / Q2 = upper) (Dietze, 2000, fig. 1) *Anatomical.* Cl, clavicle; Cr, caudal rib; Ct, cleithrum; F, femur; Fi, fibula; H, humerus; I, interclavicle; Il, ilium; Is, ischium; Mc, metacarpus; P, pelvis; Ph, phalanges; Pu, processus uncinatus; R, radius; Sc, scapula; St, stomach contents; Ti, tibia; U, ulna; Va, ventral armour.

SYSTEMATIC PALAEONTOLOGY

AMPHIBIA Linnaeus, 1758

TEMNOSPONDYLI Zittel, 1888

LIMNARCHIA Yates & Warren, 2000

STEREOSPONDYLOMORPHIA

Yates & Warren, 2000

Superfamily ARCHEGOSAUROIDEA Meyer, 1857

Family ACTINODONTIDAE Lydekker, 1885

Sclerocephalus Goldfuss, 1847

Sclerocephalus haeuseri Goldfuss, 1847

ADULT POSTCRANIAL. Vertebral column of 37-39 rhachitomous vertebrae (25 presacrals and 12-14 caudals). Neural arches high, robust, with those of the atlas-axis-complex only visible in older adults. Neural spine of the fourth cervical vertebra somewhat shorter; feature of other temnospondyls such as *Eryops* (Moulton, 1974) and *Balanerpeton* (Milner & Sequeira, 1994). Transverse processes short but prominent, posterolaterally directed, with large, vertical diapophyses. Pre- and postzygapophyses well-developed and about equal in size.

Proximal articulation surface of ribs relatively broad, because of coossification of the capitulum and tuberculum. Ribs 2-14 with a prominent processus uncinatus close to their posterior margin (Fig. 5). These processus hook-like, contacting the anterior margin of the following rib. Ribs 2-4 longest. Following ribs taper

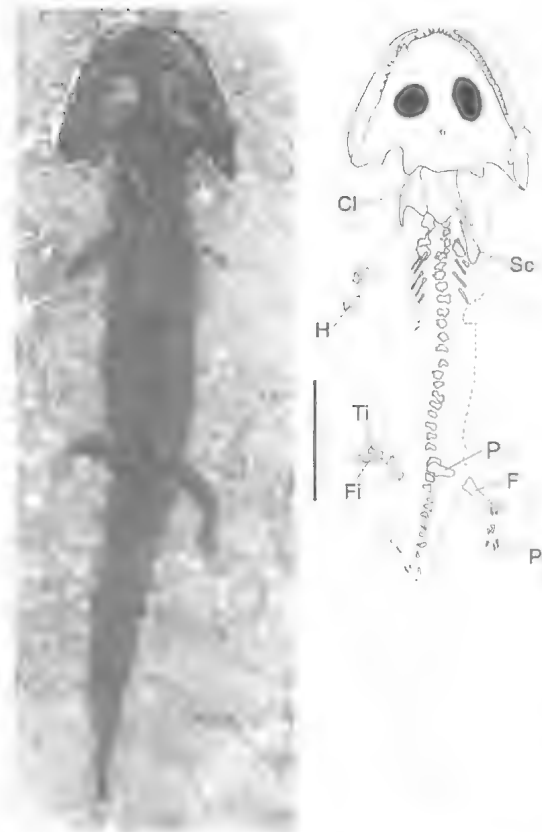


FIG. 1. Larval individual (PMNB uncataloged) in dorsal view. Scale-bar = 1cm.

slightly in length back to 14-15 vertebra and then rapidly to the pelvis. Shoulder girdle of interclavicle (which is the central ventral element) and paired clavicles, scapulocoracoid and cleithrum. Interclavicle a relatively flat bone of rhombic shape; ventral surface with numerous cristae and furrows, running from the edges to the centre. Clavicles flat, triangular, medially curved in their ventral section, broadly contact the interclavicle; dorsal process with posteriorly directed tip contacting the ventral process of the cleithra; ventrolateral margin also with some furrows. Scapulocoracoids the most prominent bones of the shoulder girdle. Shoulder blade formed as a broad, posteromedially directed, dorsal process, articulating with the clavicle antero-ventrally and with the cleithrum anterodorsally. Coracoid part of the scapulocoracoid ventrally on the posteroventral margin. Prominent glenoid surface in the posterior margin. Large supraglenoid foramen above the glenoid surface. Cleithra flat, arch-shaped, of triangular outline,

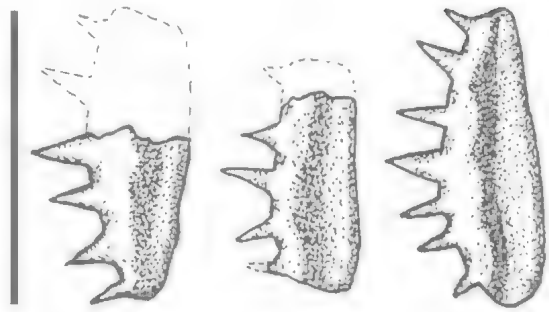


FIG. 2. Gill-teeth ('Kiemenzähne'), which were attached at the ceratobranchial filaments. Scale-bar = 1mm

contacting the scapula blade with their postero-medial margin, running ventrally out in a sharp process meeting the dorsal process of the clavicle in about the anterior mid-section of the scapula blade.

Humerus robust, moderately elongated, with tetrahedral shape (Meckert, 1993 sensu Romer, 1939) similar to the humerus of *Eryops* (Miner, 1925); proximal head prominently convex, above the processus latissimus dorsi and the crista pectoralis posteriorly and the crista dorsalis anteriorly; distal surface anteroposteriorly expanded, bearing a relatively small processus supinator and somewhat larger ectepicondylus anteriorly, as well as a very prominent entepicondylus posteriorly.

Radius and ulna relatively short elements; radius more robust, with slightly widened ends, with concave shaft; ulna more slender, with proximal part bearing the olecranon widened somewhat medially directed; olecranon very prominent, only fully ossified in older adults.

Manus well ossified in older adults, described in detail by Meckert, 1993. Phalangeal formula 2/2/3/3. On the ventral part of the body, between the interclavicle and the pelvis, there is a compact ventral armour of epidermal scales. Boy (1988) and Broili (1926) described this armour in detail. Scales generally long and sharp in the midsection and oval or circular laterally. At the level of the forelimbs, there is a prominent recess on each side of the armour. Ossification of these scales had already started in the late larval stage, in individuals with a skull length of approximately 20mm (Boy & Sues, 2000).

Pelvis very robust; ilium its most prominent element; ventral part fan-shaped anteroposteriorly bearing most of the acetabulum; dorsal part elongate-rectangular, curved posteriorly.

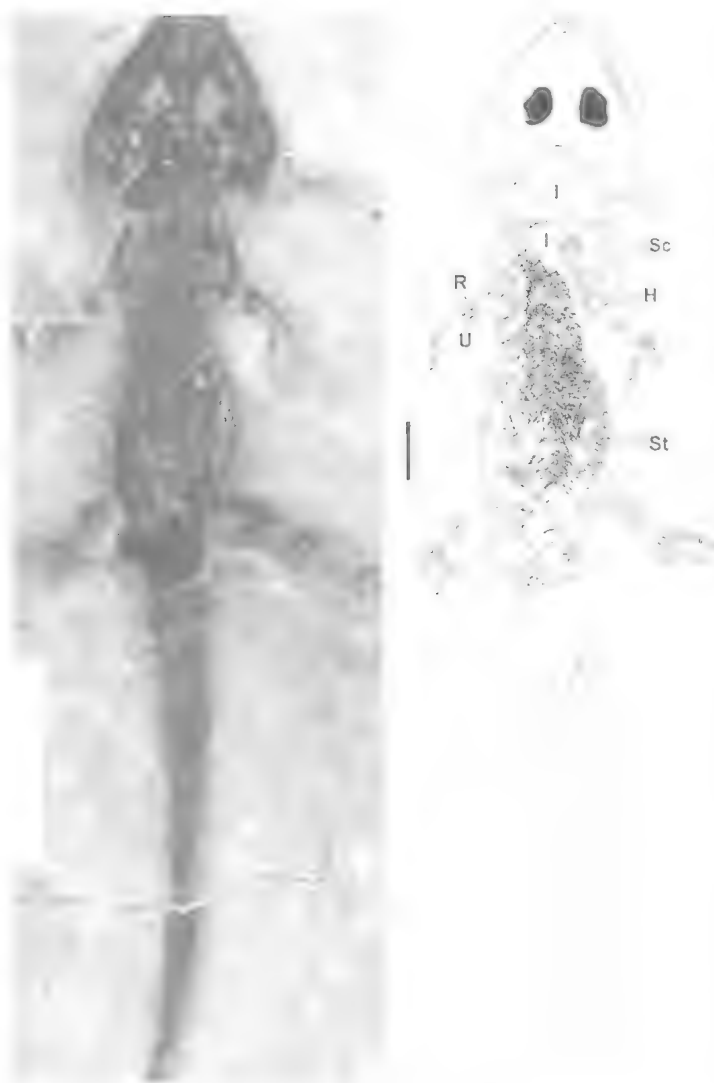


FIG. 3. Juvenile individual (PMNB uncataloged) in ventral view. In this specimen, scales of paramblypters are visible as stomach contents (St). Scale-bar=1cm.

The ventral section of the pelvic-girdle consists of the pubis and ischium, which together represent a somewhat triangular shaped plate. Hind-limbs well-developed in adults. Femur massive, rectangular, clearly the largest element of the limbs; proximal end broadened and somewhat more prominent than the distal one. Fourth trochanter weakly developed, situated proximally, with distal half of shaft still robust, terminating in a relatively straight articulation surface. Tibia and fibula much shorter than the femur; fibula somewhat shorter than tibia. Tibia less robust, with slender distal portion, contacting

the tibiale ventrally and the intermedium medially. Fibula massive, with expanded distal end with a medially directed tip. This tip touching the intermedium, while the medial margin contacts the fibulare. Metatarsals only visible in older adults. Tibiale, intermedium and fibulare very well-developed. Tibiale triangular, situated laterally, smallest of proximal metacarpals. Intermedium oval, between tibiale and fibulare; fibulare situated medially, very prominent, roughly triangular. Phalanges rod-like, terminate in a claw-shaped phalanx. Phalangeal formula varies between 2/2/3/3/3 and 2/2/2/3/3.

ONTOGENY

Four ontogenetic stages (larval, juvenile, adult and late adult) are characterised by features of the postcranial skeleton. The pectoral girdle has already been described by Meckert (1993) and the cranium by Boy (1988).

LARVAL STAGE (skull length 0.8-2.5cm). The basis for larval anatomy is an 8cm long specimen (PMNB uncataloged) (Fig. 1) with well-preserved body outlines and carbonaceous imprints of the external gill. The basibranchiale was probably cartilaginous. It ossifies in the juvenile stage and is prominently developed in adults (Boy, 1972, 1988; Boy & Sues, 2000). The ceratobranchials were arranged in up to 4 rows and

situated laterally at the level of the shoulder girdle. They probably also consisted of cartilage, but had attached to them small bony plates, so-called gill-teeth ('Kiemenzähne' after Boy, 1972) (Fig. 2). Each gill-tooth had approximately 5 spine-like denticles, which vary by 1-2 spines. Similar structures are known in *Micromelerpeton* (Boy, 1995) and *Gerrothorax* (Nilsson, 1946). The hypobranchials, hypohyals and ceratohyals were not preserved.

The limbs are conspicuous but only slightly ossified in the Bad Dürkheim specimen. The

humerus is very short and nearly quadratic; the radius and ulna are weakly developed, but the radius is longer. Elements of the manus are not recorded and were probably cartilaginous. The femur is rectangular in lateral view, relatively short, very robust and longer than the less developed tibia and fibula. Elements of the pes are badly preserved. The centra are rhachitinous and bear paired neural arches with low neural spines (Boy, 1972). Ribs of vertebrae 1-14 are ossified, rod-like and slightly broadened proximally. Capitulum and tuberculum not clearly developed. The sacral rib is slender. Caudal ribs have not been recorded. The pelvis is relatively weak and not as robust as the well-developed shoulder-girdle (Meckert, 1993). The tail occupies approximately 50% of body length. No stomach contents could be found.

JUVENILE STAGE (skull length 3.5-7.5cm). Representative juvenile is a 26cm long specimen with clearly visible body-outlines (PMNB uncataloged) (Fig. 3). The external gill has been lost and limbs are more ossified. The humerus shows no major differences to that in the larval stage. Radius and ulna are about as long as the humerus. Radius and ulna are approximately equal in length, but the radius is somewhat more robust. The femur is elongate-rectangular with slightly expanded proximal and distal ends. It is clearly more robust and about twice as large as the tibia and fibula. The tibia is rod-shaped and slightly expanded distally. The metapodials are not ossified; phalanges are clearly visible. Claw-like terminal phalanges are developed. GMS 394 shows that the vertebrae are well-ossified and bear lower neural arches and spines as in adults. The ribs are more robust than in the larval individual. The 2nd to 14th presacral ribs are club-like and broadened laterally. Between 12 and 14 caudal ribs are presented. The second and third ribs, distal to the sacral rib, are longest. The

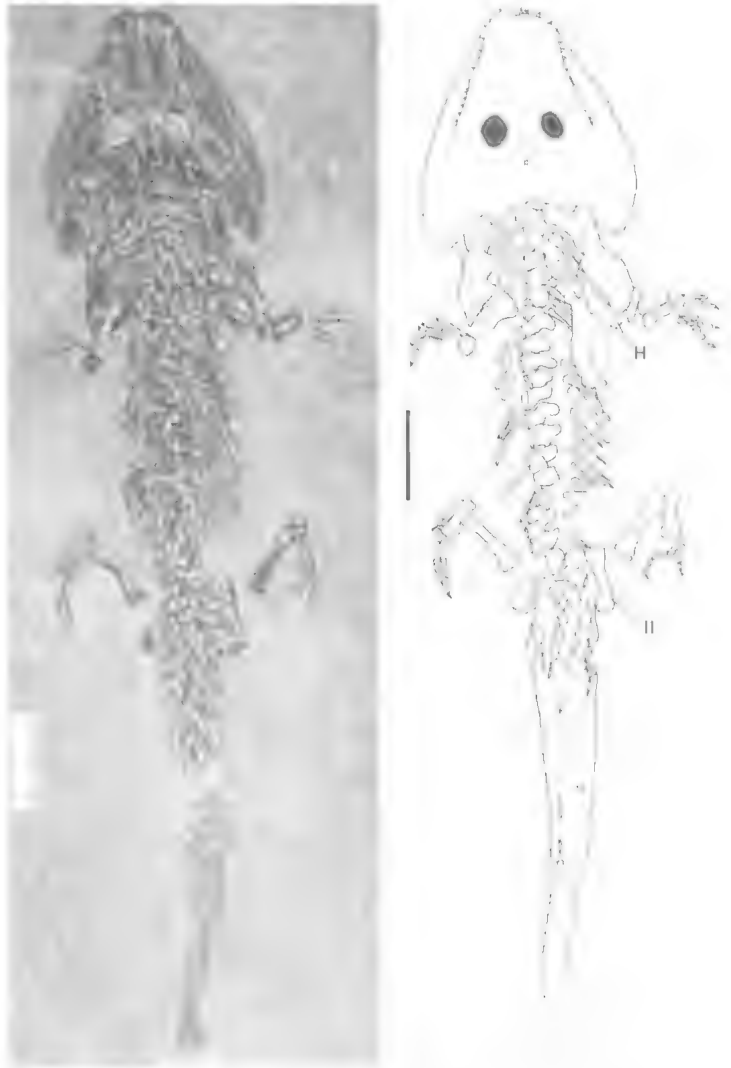


FIG. 4. Adult individual (PMNB PDC-327) in dorsal view. Scale-bar = 5cm.

tail occupies about 45% of body length, but is shorter than in larval individuals.

ADULT STAGE (skull length 9.5-16cm). The representative adult is a well-preserved skeleton 74cm long (PMNB-PDC 327) (Fig. 4). In general, the body has become somewhat more compact. The humerus is robust, but not as stout as in juveniles. Its proximal and distal ends are still cartilaginous (Broili, 1926; Boy, 1988). Ulna and radius are about equal in length, but the radius is more robust. In both, the shaft is inwardly curved, with the ulna showing a more prominent inflexion. Phalanges are broader than



FIG. 5. Late adult individual (PMNB BGC-112) in lateral view. In this stage the ventral armour (Va) is clearly visible. Scale-bar = 20cm.

in juveniles and still not completely ossified. Also the metacarpus is not completely ossified. The hind-limb elements are similar in shape to those in the juvenile specimens, but are more robust. Metatarsals are present.

Vertebrae are well-developed. The pleurocentra are slender and of rhachitinous shape (Schoch, 1999: 107). Boy (1988) described the intercentra as unpaired with a low semicircular shape and the neural arches as robust and

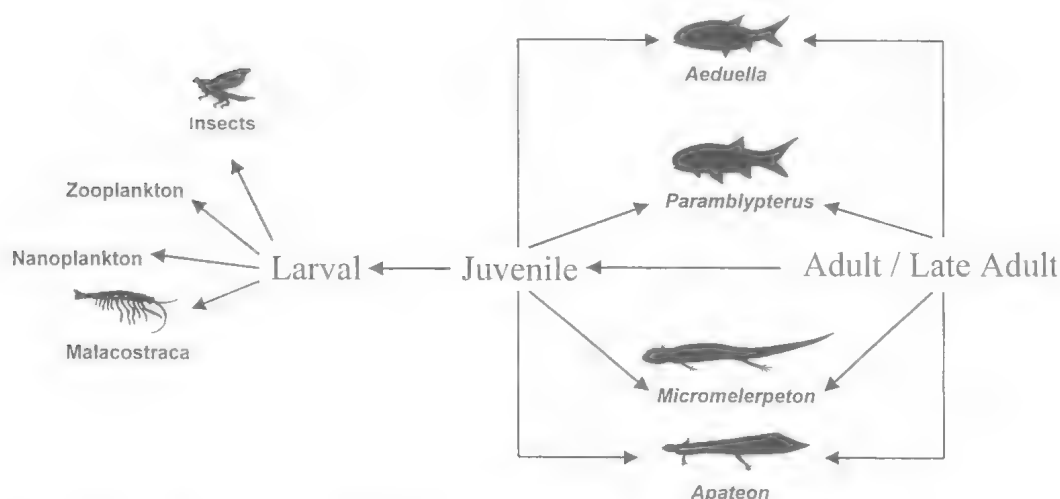


FIG. 6. Proposed food chain of *Sclerocephalus* in the larval, juvenile and adult/late adult stage.

relatively high. This could also be observed on PMNB-PDC 327.

All ribs are strongly developed and have a co-ossified capitulum and tuberculum. This is especially visible in ribs 2-14 where the proximal ends are broadened into a club-like shape. These ribs bear a hook-like processus uncinatus posteriorly. In large individuals, there are lateral depressions on ribs 2-6. Pelvic- and shoulder-girdles are robust and the pelvis is now completely ossified. The tail is shorter than in juveniles. It occupies about 40% of body-length.

LATE ADULT STAGE (skull length >18cm). The late adult stage is based on PMNB-BGC 112 (Fig. 5). In general the body is shorter than in earlier stages and all bones are well ossified. Humeri are robust and slightly elongated. Metapodials are completely ossified. Of the atlas-axis-complex only the neural arches are visible. Tuberosities on the proximal ends of the ribs change from being club- to bow-shaped and can be observed to rib 7 (but possibly extended to 9). Also the lateral depressions, mentioned for the adults, can be recorded to ribs 7-9, and are deeper. The pelvis is extremely robust. The tail is shorter than in earlier stages, but does not differ much from that of adults (it also occupies 40% of body-length).

HABITAT RECONSTRUCTION

During the Lower Permian, the Saar-Nahe Basin in SW Germany was traversed by several river systems. In some areas water was trapped in low relief, forming lakes (Dietze, 1999). These

lakes (Table 1) normally existed only for a relatively short geological period, but contained a well-balanced ecosystem (palaeocommunities after Boy, 1998 sensu Järvinen et al., 1986), composed of large amphibians (e.g. the limnarchian *Archegosaurus*), small amphibians (e.g. the branchiosaur *Micromelerpeton* and *Apateton*), large fishes (e.g. the xenacanthoidian freshwater sharks *Xenacanthus* and *Orthacanthus*), small fishes (e.g. the amblypterid *Paramblypterus* or the acanthodian *Acanthodes*), as well as a variety of different invertebrates (e.g. ostracods, bivalves, shrimps) (Boy, 1998). One of the larger lakes was Lake Humberg (L-O 10) that extended over an area of 3,400km² and deposited nearly the whole Saar-Nahe Basin (Stapf, 1990). Boy (1994) mentioned, that lake deposits from Lake Humberg can be divided into 4 phases.

TABLE 1. Distribution of the ontogenetic stages of *Sclerocephalus haeuseri* in different lake localities (primary based on unpublished excavation reports of the Pfalzmuseum für Naturkunde, Bad Dürkheim).

Layer	Lake	Lake-size (km ²)	Larval	Juv.	Adult	Late Adult
L-O 10	Rümmelbach-Humberg	ca. 3400	14	ca.100	0	0
L-O 9	Ruthweiler	ca. 10	21	0	0	0
L-O 8	Odernheim	ca. 760	31	ca.100	2	0
L-O 7	Jeckenbach-Heimkirchen	ca. 230	0	4	ca.50	8
L-O 6	Niederkirchen	ca. 40	0	2	2	2
Q 2	Quirnbach	ca. 500	0	0	0	1
Q1	St Wendel	ca. 40	0	2	20	3

Sclerocephalus is found (together with *Paramblypterus uvernoyi* and *Apateon pedestris*) only in the first phase, when the Lake was deepest. In other lakes, such as in Lake Odernheim (L-O 8), *Sclerocephalus* was found together with the large branchiosaur *Micromelerpeton* (Boy, 1994) or with the small freshwater shark *Triodus* (Lake Klauswald, L-O 9, after Dietze, 1999).

Boy (1988) concluded that juvenile *Sclerocephalus* individuals might have lived in shallow lakes. We suggest that juvenile *Sclerocephalus* lived in large, relatively deep lakes of the Rümmlbach-Humberg type. Recent extensive excavations by the Pfälzmuseum für Naturkunde in Bad Dürkheim in the corresponding localities Gresaubach/Lebach and Humberg/Odernheim (Top L-O 10) support this suggestion as only larval and juvenile individuals have been found. It therefore is suggested that these lakes were being used as spawning grounds whilst adult individuals lived in another environment. Also, this could explain why, in lakes where adult and late adult individuals are common, as in Lake Jeckenbach (L-O 6) (Stapf, 1990), larval and juvenile individuals are rare or absent.

DIET DURING ONTOGENY

As mentioned above, no stomach contents could be associated with the larval specimens. Most probably their diet consisted of plankton and malacostracans (as the common *Uronectes*) or maybe small insects. Boy (1993) suggested that larval *Sclerocephalus*, similar to some recent amphibians could have caught its prey with a suck-snap method (Bramble & Wake, 1985). Juveniles caught large prey. As mentioned above, a complete, large *Paramblypterus* with its head folded backwards was found in the stomach of PMNB (uncataloged). Altogether 6 fish-bearing specimens were observed (only one in a public collection, PMNB, uncataloged, fig. 3); another one (GPIM-N 1166) was mentioned by Boy (1988). We therefore conclude that *Sclerocephalus* swallowed these fishes whole. In numerous specimens, scales of paramblypterids, and also traces of small amphibians such as *Apateon* and *Micromelerpeton*, have been found. As a rarity, the stomach of 1 specimen (GMS, uncataloged) contained remains of a smaller *Sclerocephalus*. This is the first record of cannibalism in this taxon.

Adult and late adult individuals were primary piscivores, in which *Paramblypterus* represents the common prey. Observations of stomach contents and a large number of coprolites showed

that smaller amphibians and probably smaller *Sclerocephalus* individuals also belonged to the prey. Acanthodians were never present as stomach contents or in the coprolites. These fishes were very common in the environment of *Sclerocephalus* and of moderate size, but had large spines anterior to their fins. It is possible that the more heavily built adult and late adult *Sclerocephalus* individuals mostly did not hunt actively, but watched for prey next to the shore and caught them with the suck-snap method. If we accept this premise, *Paramblypterus* and small amphibians would have been an easier prey than the spine-bearing acanthodians.

CONCLUSIONS

In the first ontogenetic phases, *Sclerocephalus haeuseri* was well adapted to its aquatic habit,



FIG. 7. Idealised reconstruction of the four ontogenetic stages: A, larval; B, juvenile; C, adult; and D, late adult. The right side of the body shows the dorsal bones, the left side shows the ventral elements.

which is especially perceptible in the slender shape of the body, the weakly ossified limbs and the long rudder-tail. Larval individuals are up to 10cm in length. Their jaws were not very strong and bore only slightly developed teeth (Boy, 1988); therefore their diet must have consisted of plankton and probably insects or malacostracans.

In the juvenile stage, individuals could reach to 50cm long. They still had a slender body-shape and a long tail and probably were active hunters. Stomach contents and coprolites contain remains of paramblypterids and small amphibians, including smaller individuals of *Sclerocephalus*. The prey was swallowed entirely. It is conspicuous that some lakes, especially those of the 'Rümmelbach-Humberg-Lake' type, nearly exclusively yielded larval and juvenile individuals (up to the late juvenile stage (= late 'metamorphic' stage after Boy & Sues, 2000) or subadult stage (Table 1). We therefore conclude that adult *S. haeuseri* might have changed their habit from fully aquatic to amphibious. Adults probably visited the habitat of the younger ones to spawn; therefore they are rarely recorded in these layers. According to Boy (1998) both juvenile and adult / late adult individuals were the so-called top-predators in their environment (Fig. 6). In Lake Niederkirchen *Sclerocephalus* shared this position with the freshwater shark *Orthacanthus senckenbergensis*. In Lake Humberg, as mentioned above, *Sclerocephalus* was only recorded in the first of 4 phases. In the second phase the position as top-predator was held by the freshwater shark *Xenacanthus meisenheimensis* (Boy, 1994), while in the fourth phase the top-predator position was shared by the archegosaurids *Archegosaurus* and *Cheliderpeton*. The latter is the closest relative to *Sclerocephalus* (Yates & Warren, 2000) and is also known in different ontogenetic stages (Boy, 1993; Steyer, 2000).

In the adult/late adult stage, *Sclerocephalus* specialised on paramblypterids, but also caught smaller amphibians such as *Apateon* or *Micromelerpeton*. Although *Acanthodes* was very common in the lakes, it was not recorded in the stomach contents or coprolites and therefore probably was not preyed upon. The limbs were well ossified in the adult stage, so that these individuals also could have been terrestrial from time to time.

ACKNOWLEDGEMENTS

UL is grateful to Bernd Graumann (formerly Pfalzmuseum für Naturkunde, Bad Dürkheim),

Klaus Krätschmer (Oderheim), Rainer Schoch (Staatliches Museum für Naturkunde, Stuttgart), and Jürgen Boy, Karl Stapf and Jahn Hornung (University of Mainz) for fruitful discussions and access to the specimens under their care. SS thanks Scott Hocknull (Queensland Museum) and Anne Warren (La Trobe University, Melbourne) for helpful discussions during writing and for reviewing and commenting upon the manuscript. He is also grateful to James Cox (Brisbane) for making the drawings of Fig. 6.

LITERATURE CITED

- AMMON, L. v. 1889. Die permischen Amphibien der Rheinpfalz. (Straub Verlag: Munich).
- BOY, J. A. 1972. Die Branchiosaurier (Amphibia) des saarpfälzischen Rotliegenden (Perm, SW-Deutschland). Abhandlungen des hessischen Landesamtes für Bodenforschung 65: 1-137.
1974. Die Larven der rhachitomen Amphibien (Amphibia: Temnospondyli; Karbon-Trias). Paläontologische Zeitschrift 48: 236-268.
1976. Überblick über die Fauna des saarpfälzischen Rotliegenden (Unter-Perm). Mainzer geowissenschaftliche Mitteilungen 5: 13-85.
1988. Über einige Vertreter der Eryopidea (Amphibia: Temnospondyli) aus dem europäischen Rotliegend (?höchstes Karbon - Perm) 1. *Sclerocephalus*. Paläontologische Zeitschrift 62(1/2): 107-132.
1990. Über einige Vertreter der Eryopidea (Amphibia: Temnospondyli) aus dem europäischen Rotliegend (?höchstes Karbon - Perm) 3. *Onchiodon*. Paläontologische Zeitschrift 64(3/4): 287-312.
1993. Über einige Vertreter der Eryopidea (Amphibia: Temnospondyli) aus dem europäischen Rotliegend (?höchstes Karbon - Perm) 4. *Cheliderpeton latirostre*. Paläontologische Zeitschrift 62(1/2): 123-143.
1994. Seen der Rotliegend-Zeit - Ein Lebensraum vor rund 300 Millionen Jahren in der Pfalz. Pp. 107-116. In Koenigswald, W.v. & Meyer, W. (eds) Erdgeschichte im Rheinland. (Verlag Dr Pfeil: Munich).
1995. Über die Micromelerpetontidae (Amphibia: Temnospondyli). 1. Morphologie und Paläoökologie des *Micromelerpeton credneri* (Unter-Perm; SW-Deutschland). Paläontologische Zeitschrift 69: 429-457.
1998. Möglichkeiten und Grenzen einer Ökosystem-Rekonstruktion am Beispiel des spätpaläozoischen lakustrinen Paläo-Ökosystems. Paläontologische Zeitschrift 72(1/2): 207-240.
- BOY, J.A. & FICHTER, J. 1982. Zur Straigraphie des saarpfälzischen Rotliegenden (?Ober-Karbon - Unter-Perm; SW-Deutschland). Zeitschrift der deutschen geologischen Gesellschaft 133: 607-642.
- BOY, J.A. & SUES, H.-D. 2000. Branchiosaurs: Larvae, metamorphosis, and heterochrony in

- temnospondyl and seymouriamorph amphibians. Pp. 1150-1197. In Heatwole, H. & Carroll, R.L. (eds) *Amphibian Biology* Vol. 4 (Surrey Beatty & Sons: Chipping Norton).
- BRAMBLE, D.M. & WAKE, D.B. 1985. Feeding mechanics of lower tetrapods. Pp. 230-261. In Hildebrand, M., Bramble, D.M., Liem, K.F. & Wake, D.B. (eds) *Functional Vertebrate Morphology* (Belknap Press: Cambridge).
- BRANCO, W. 1887. *Weissia bavarica* g. n. sp. n., ein neuer Stegocephale aus dem unteren Rothliegenden. Jahrbuch der königlich Preussischen geologischen Landesanstalt und Bergakademie Berlin 1886: 22-39.
- BROILI, F. 1908. Ueber *Sclerocephalus* aus der Gaskohle von Nürschan und das Alter dieser Ablagerungen. Jahrbuch der kaiserlich königlichen geologischen Reichsanstalt Wien 58: 49-70.
1926. Über *Sclerocephalus Häuseri* GOLDFUSS. Sitzungsberichte der Bayerischen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Abteilung 1926: 199-222.
- BULMAN, O.M. 1928. Additional notes on some branchiosaurs from Odernheim. Annals and Magazine of Natural History 10: 250-255.
- BURMEISTER, H. 1850. Die Labyrinthodonten aus dem Saarbrücker Steinkohlengebirge. (Berlin)
- CREDNER, H. 1882. Die Stegocephalen und Saurier aus dem Rothliegenden des Plauen' schen Grundes bei Dresden. III. Theil. Zeitschrift der deutschen geologischen Gesellschaft 34: 213-237.
1885. Die Stegocephalen und Saurier aus dem Rothliegenden des Plauen' schen Grundes bei Dresden. V. Theil. Zeitschrift der deutschen geologischen Gesellschaft 37: 694-736.
1886. Die Stegocephalen und Saurier aus dem Rothliegenden des Plauen' schen Grundes bei Dresden. VI. Theil. Zeitschrift der deutschen geologischen Gesellschaft 38: 576-632.
1893. Die Stegocephalen und Saurier aus dem Rothliegenden des Plauen' schen Grundes bei Dresden. X. Theil. Zeitschrift der deutschen geologischen Gesellschaft 45: 639-704.
- DIETZE, K. 1999. *Paramblypterus duvernoyi* (Actinopterygii): Skull morphology and intra-specific and its implications for the systematics of paramblypterid fishes. Journal of Vertebrate Paleontology 19(2): 247-262.
2000. A revision of paramblypterid and amblypterid actinopterygians from Upper Carboniferous - Lower Permian lacustrine deposits of Central Europe. Palaeontology 43(5): 927-966.
- FRITSCH, A. 1901. Fauna der Gaskohle und der Kalksteine der Permformation Böhmens. 4. Volume. (self published: Prague).
- GEINITZ, H.B. 1861. Dyas, oder die Zechsteinformation und das Rothliegende. Heft 1. Die animalische Ueberreste der Dyas. VII-XVIII: 1-342.
- GOLDFUSS, G.A. 1847. Beiträge zur vorweltlichen Fauna des Steinkohlgebirges. Verhandlungen des naturhistorischen Vereins für Rheinlande und Westphalen: 1-27.
- HEYLER, D. 1975. Sur les *Branchiosaurus* et autres petits amphibiens apparentés de la Sarre et du bassin d'Autun. Bulletin Trimestriel de la Société d'Histoire Naturelle et des Amis du Museum d'Autun 75: 15-27.
- JÄRVINEN, O., BABIN, C., BAMBACH, R., FLÜGEL, E., FÜRISCH, F., FUTUYMA, D., NIKLAS, K., PANCHEN, A., SIMBERLOFF, D., UNDERWOOD, A. & WEIDICH, K. 1986. The neontologico-paleontological interface of community evolution: How do the pieces in the kaleidoscopic biosphere move? Pp. 331-350. In Raup, D.M. & Jablonski, D. (eds) *Patterns and processes in the history of life* (Springer-Verlag: Berlin).
- JORDAN, H. 1849. Ergänzende Beobachtungen zu der Abhandlung von GOLDFUSS über die Gattung *Archegosaurus*. Verhandlungen des naturhistorischen Vereins für Rheinlande und Westphalen 6: 76-81.
- MECKERT, D. 1993. Der Schultergürtel des *Sclerocephalus haeuseri* GOLDFUSS, 1847 im Vergleich mit *Eryops* COPE, 1877 (Eryopidea, Amphibia, Perm). Palaeontographica (A)229: 113-140.
- MEYER, H. v. 1857. Reptilien aus der Steinkohlen-Formation in Deutschland. Palaeontographica 6: 59-220.
1858. Nachtrag zu den Reptilien aus der Steinkohlen-Formation in Deutschland, insbesondere zu *Archegosaurus latirostris*. Palaeontographica 6: 219-220.
- MINER, R.W. 1925. The pectoral limb of *Eryops* and other primitive tetrapods. Bulletin of the American Museum of Natural History 51: 145-312.
- MILNER, A.R. & SEQUEIRA, S.E.K. 1994. The temnospondyl amphibians from the Viséan of East Kirkton, West Lothian, Scotland. Transactions of the Royal Society of Edinburgh: Earth Sciences 84: 331-361.
- MOULTON, J.M. 1974. A description of the vertebral column of *Eryops* based on the notes and drawings of A.S. Romer. Breviora, 428: 1-44.
- NILSSON, T. 1946. A new find of *Gerrothorax rhaeticus* Nilsson, a plagiosaurid from the Rhaetic of Scania. Lunds Universitet Arsskrift, N.F. 42: 1-42.
- ROMER, A.S. 1939. Notes on branchiosaurs. American Journal of Sciences 237: 748-761.
1947. Review of the Labyrinthodontia. Bulletin of the Museum of Comparative Zoology, Geological Series 99: 1-368.
- SEQUEIRA, S.E. & MILNER, A. 1993. The temnospondyl amphibian *Capetus* from the Upper Carboniferous of Czech Republic. Palaeontology 36(3): 657-680.

- SCHOCH, R.R. 1999. Comparative osteology of *Mastodonsaurus giganteus* (JAEGER, 1828) from the Middle Triassic (Lettenkeuper: Longobardian) of Germany (Baden-Württemberg, Bayern, Thüringen). Stuttgarter Beiträge zur Naturkunde (B) 278: 1-175.
- STAPF, K.R. 1990. Fazies und Verbreitung lakustriner Systeme im Rotliegend des Saar-Nahe-Beckens (SW-Deutschland). Mainzer geowissenschaftliche Mitteilungen 19: 213-234.
- STEYER, J.-S. 2000. Ontogeny and phylogeny in temnospondyls: a new method of analysis. Zoological Journal of the Linnean Society 130: 449-467.
- THEOBALD, N. 1958. Contribution à l'étude des stégocéphales du Permien inférieur de la Sarre. Annales Universitatis Saraviensis, Naturwissenschaftliche Reihe (7)2: 192-210.
- WATSON, D.M.S. 1919. The structure, evolution and origin of the Amphibia. – The 'order' Rhachitomi and Stereospondyli. Philosophical Transactions of the Royal Society of London (B)209: 1-73.
1963. On growth stages in branchiosaurs. Palaeontology 6: 540-553.
- WERNEBURG, R. 1983. Stegocephalen (Rhachitomi, Amphibia) aus dem hohen Unterrotliegenden (Oberhöfer Schichten) des Thüringer Waldes. Freiburger Forschungshefte (C)384: 111-129.
1988. Paläobiogeographie der labyrinthodonten Amphibien im Oberkarbon und Rotliegenden Mitteleuropas. Zeitschrift der geologischen Wissenschaften 16: 929-932.
1989. Labyrinthodontier (Amphibia) aus dem Oberkarbon und Unterperm Mitteleuropas – Systematik, Phylogenie und Biostratigraphie. Freiburger Forschungshefte, Reihe (C)436: 7-57.
1992. *Sclerocephalus jogischneideri* n. sp. (Eryopidea, Amphibia) aus dem Unterrotliegenden (Unterperm) des Thüringer Waldes. Freiburger Forschungshefte (C)445: 29-48.
1993. *Onchiodon* (Eryopidae, Amphibia) aus dem Rotliegend des Innersudetischen Beckens (Böhmen). Paläontologische Zeitschrift 67(3/4): 343-355.
- YATES, A.M. & WARREN, A.A. 2000. The phylogeny of the 'higher' temnospondyls (Vertebrata: Choanata) and its implications for the monophyly and origins of the Stereospondyli. Zoological Journal of the Linnean Society 128: 77-121.



A NEW SPECIES OF *CALAMOECIA* (COPEPODA: CALANOIDA) FROM ARID AUSTRALIA, WITH COMMENTS ON THE CALANOID COPEPODS OF THE PAROO, NORTHWESTERN MURRAY-DARLING BASIN

BRIAN V. TIMMS

Timms, B.V. 2001 06 30: A new species of *Calamoecia* (Copepoda: Calanoida) from arid Australia, with comments on the calanoid copepods of the Paroo, northwestern Murray-Darling Basin. *Memoirs of the Queensland Museum* 46(2): 783-790. Brisbane. ISSN 0079-8835.

Calamoecia baylyi sp.nov. is described from claypans in the Paroo catchment in southwestern Qld and northwestern NSW. It also occurs in WA where it was previously known as the Cue form of *C. lucasi*. Ten species of calanoid copepod occur in the Paroo with *Boeckella triarticulata*, *C. canberra* and *C. lucasi* common, *B. fluvialis* and *C. zeidleri* present and *B. robusta robusta*, *B. timmsi*, *C. baylyi*, *Diaptomus lumholtzi* and *Gladioferens spinosus* uncommon. Co-occurrences are common, especially in claypans and riverine waterholes. □ *New species, Calamoecia, Calanoid copepods, environmental ecology, biogeography.*

Brian V. Timms, School of Geosciences, University of Newcastle, Callaghan 2308, Australia (e-mail: ggbvt@alinga.newcastle.edu.au); 28 March 2001.

Calamoecia Brady contains 16 species (Bayly, 1992, 1998; Halse & McRae, 2001). Two of the most recent additions, *C. zeidleri* Bayly and *C. halsei* Bayly live in waters in remote parts of arid Australia. Also occupying some of these waters is a form similar to *C. lucasi* Brady but different enough to be recognised as the Cue form (Bayly, 1984). It has been reported from Cue (Bayly, 1984), near Port Hedland (Timms & Morton, 1988), and the Gascoyne-Murchison (Bayly, 1998), all in NW WA. Although Bayly (1998) thought this western form of *C. lucasi* was a new species, he was reticent to proceed partly because it is allopatric with *C. lucasi* s.s. (I.A.E. Bayly, pers. comm.). *C. lucasi* s.s. is widespread in eastern and central Australia (Maly & Bayly, 1991), but records of *C. lucasi* in WA in Maly & Bayly (1991) and in Maly et al. (1997) refer to its western form (alias Cue form) (Maly & Bayly, 1991, and S. Halse, pers. comm.). However *C. lucasi* s.s. occurs at Lake Gregory, S Kimberley (Halse et al., 1998) and another variant of *C. lucasi*, the 'Lake Grace form' lives near Lake Grace in SW WA.

Discovery of populations similar to the Cue form in the Paroo, NW NSW and SW Qld, and sympatric with *C. lucasi* s.s. confirmed that the Cue form is a separate species. Not only are there many differences between it and *C. lucasi* s.s., but the Cue form has maintained its distinctiveness despite chances for interbreeding.

The Paroo area contains 9 other calanoid copepods including many inland forms for which few

ecological data are available. Ecological and biogeographic studies on Australian calanoid copepods (Bayly, 1996; Maly, 1984; Maly & Bayly, 1991; Maly & Maly, 1997; Maly et al., 1997; Timms & Morton, 1988; Walsh & Tyler, 1998) have not included data from the eastern arid zone.

The aims of this paper are to describe the Cue form of *Calamoecia lucasi* s.l. and to comment on ecological biogeography of calanoid copepods in the Paroo catchment of the NW Murray-Darling Basin.

METHODS

Specimens were measured under a Wild M3C stereomicroscope fitted with an eyepiece micrometer, stained with Chorazol Black, and dissected with tungsten needles in DePeX mountant on a microslide under the same microscope. Appendages were studied and drawn using a Olympus BHA microscope fitted with Olympus drawing attachment. Terminology and abbreviations used in describing the appendages follow Bayly (1992).

Ecological data on the copepods of the Paroo are gleaned from my monitoring studies of 100+ wetland sites over 13 years (Timms 1993, 1997a, 1997b, 1998; unpubl. data). The area covered ranges from Currawinya National Park in the N (centred on 144°25'E, 28°50'S) to Lake Peery in the Overflow lakes area (143°37'E, 30°45'S) and encompassing about two-thirds of the Paroo's catchment of 73, 600km².

SYSTEMATICS

Class CRUSTACEA

Order COPEPODA

Family CENTROPAGIDAE Giesbrecht

Calamoeccia Brady*Calamoeccia baylyi* sp. nov.

(Figs 1, 2)

Calamoeccia lucasi Brady; Bayly, 1984 (in part, the Cue population, fig. 4A-D).

ETYMOLOGY. In honour of Dr Ian A.E. Bayly, to whom so much is owed on the taxonomy and ecology of centropagid copepods.

MATERIAL. HOLOTYPE ♂ QMW25483, length 0.77mm prosome, 1.19mm total, ALLOTYPE ♀ QM W25484, length 1.10mm prosome, 1.52mm total, both mounted on microslides in DePeX., PARATYPES 30 ♂s, 20 ♀s QMW25485, Queensland Museum. Collected by the author on 17 May, 1996. OTHER MATERIAL. 30 ♂s, 15 ♀s QM W25487, Turkey Pan, 29°33'S, 144°49'E, Bloodwood Station, 130km NW of Bourke, NSW, collected by the author, 19 May, 1998; 5 ♂s, 3 ♀s, Melaleuca Pan, 29°33'S, 144°48'E, Bloodwood Station, NSW, collected by author 19 May 1998; a claypan near S end of Lake Wyara, Currawinya National Park, 28°48'S, 144°15'E, Qld, collected by author 14 May, 1996; dissected ♂ WAM C24994 and vial of 10 ♂s and 10 ♀s WAM C24996 from an unnamed claypan, 24°47'35"S, 114°09'14"E (CB 58e of Halse et al., 2000), collected S.A. Halse 25 July 1995; dissected ♀ WAM C24995 from Tirigie Claypan, 24°38'34"S, 113°59'29"E, collected by S. Halse 17 August, 1994.

TYPE LOCALITY. A claypan 1.5km NE of Coomburra Waterhole, Currawinya National Park, 28°47'E, 144°22'E, SW Queensland.

DESCRIPTION. *Male*. On first legs, outer edge spines on exopodite proximal segment (Re1) and distal segment (Re3) with abnormally large secondary spinules (same in females [Fig. 1A]). On fifth leg (Fig. 1B,C) distal basidopodite segment (B2) with a distinct space between insertion of exopodite and endopodite, which in the right limb is wider and a little indented. Proximal segment of right exopodite (Re1) somewhat cuboidal with a spine on its outer distal corner and a small rounded protrusion on its inner distal corner. Middle distal segment (Re2) with a prominent rounded projection midway on its inner surface. Claw (Re3) strongly bent about one-quarter way along its length, and lacking an inner spine. Right endopodite (Ri) 3-segmented, proximal (Ri1) and middle segment (Ri2) round-oval shaped, but distal segment (Ri3) more elongated and bearing 2 long setae subterminally. Left exopod (Re) 1-segmented with a small spine

two-thirds along outer margin and tip expanded into rounded spade-like structure with denticles on and towards its margin. Base of this structure with short spine on a protuberance on the inner side and longer spine next to it. Left endopodite (Ri) 1-segmented, a little longer than the first 2 segments of the right exopodite (i.e. exopodite without its claw), with almost parallel sides. This segment with 5 spines (2 terminal, 3 subterminal) decreasing almost uniformly in length from the inner spine to outermost one.

Female. On first legs (Fig. 1A), spine on outer edge of proximal segment (Re1) and 2 spines on outer edge of distal segment (Re3) of exopodite with abnormally large secondary spinules (as in ♂). These outer spines absent on exopods of legs 2-4. On fifth leg (Fig. 1D), proximal exopodite segment (Re1) with an outer spine with secondary spinules. Middle exopodite segment (Re2) also with such a spine and a large curved slender outgrowth on its distal inner corner. This outgrowth with 2 rows of spinules. Distal exopodite segment (Re3) with 5 or 6 spines, outermost with secondary spinules, next inner one longest but still a little shorter than the segment. Curved outgrowth on Re2 subequal to Re3 plus its spines. Endopodite (Ri) 1-segmented, with 7 or 8 long setae (4 or 5 on inner side, 1 terminal, and 2 on outer edge.). Prosome terminating in elongated lobes on either side of prosome-urosome junction (Fig. 1E,F). Urosome (Fig. 1E,F) with genital segment about 1.5 × as long as wide. Genital operculum with a distinct nipple and on a large mound. Left side of genital segment with a bulge almost halfway along its length, but no indication of an associated furrow.

REMARKS. *Variation between populations*. Specimens from the Carnarvon region of WA are slightly different from the type material in a number of features. On the ♂ fifth leg, the spine of the outer distal corner of the first exopodite segment (Re1) is much longer (Fig. 2B). The claw of the right exopodite (Re3) is markedly bent further along its length than in type material (ca one-third to halfway along its length). The right endopodite is curved inwards and the first and second segment (Ri1, Ri2) even more bulbous so that especially the second segment presents a semicircular outer edge (Fig 2B). In the ♀ the most noticeable difference is on the third segment of the exopodite (Re3) where spines (6 instead of 5) are longer than in the type material, so that they exceed the length of the segment and of the curved inner process of the

second segment (Re2) (Fig. 2A). Bayly (1998) thought different material he examined from the Carnarvon region 'agreed exactly with the Cue population', i.e. was the form now known as *C. baylyi*.

The Cue population of *C. lucasi* s.l. studied by Bayly (1984) is almost identical to the type material from the Paroo. Like the Carnarvon population the second segment of the right endopodite (Ri2) in ♂ is enlarged and with a semicircular outer edge, and in ♀ the proportions and lengths of the spines on the third exopodite segment are the same. (Fig. 2C; Bayly, 1984, fig. 4). The Cue population is similar to the Paroo type material in other features, including the short spine at the outer distal corner of the first right exopodite segment (Re1) and the marked bend in the right exopod claw (Re3) being about a quarter to a third along its length. Both these western populations of *C. lucasi* s.l. are considered as belonging to *C. baylyi*.

The Lake Grace population of *C. lucasi* s.l. studied by Bayly (1984) exhibits most of the features of *C. baylyi* including most of the minor modifications seen in the Carnarvon and Cue material. It has however some curious features unique to it, including an outgrowth on the inner distal corner of the proximal segment of the right exopodite (Re1). This is much more prominent than the usual small rounded protrusion in typical *C. baylyi*, but not as long as in *C. elongata*, the only other species with an outgrowth in this position. Also unique to this population is the variable setation on the distal segment of the right endopodite (Ri3) so that generally the 2 setae are of very unequal lengths and usually much reduced. In addition some of the features typical of *C. baylyi* are either not as well developed (e.g.

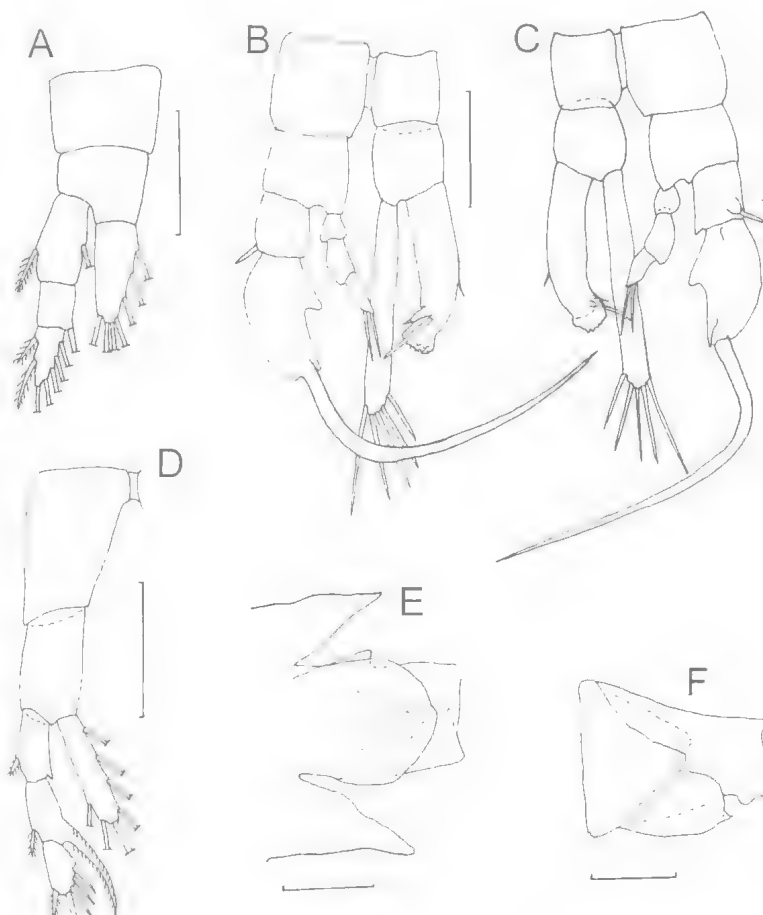


FIG. 1. *Calamoecia baylyi* sp. nov.; A, ♀ first leg; B & C, anterior and posterior aspects, respectively, of ♂ fifth legs; D, ♀ fifth leg; E, ventral aspect of ♀ genital segment with lobes of last prosomal segment; F, left lateral aspect of ♀ genital segment with lobes of last prosomal segment. B and C from holotype, A, D, E, F from allotype. Scale bars = 0.1 mm.

the projection midway along the inner surface of the middle right exopodite (Re2) is hardly developed) (Fig. 2D), or more developed (e.g. the outgrowth on the left side of the genital segment is more pronounced) (Bayly, 1984, fig. 5E,F). This Lake Grace material should be considered as *C. baylyi*, though a little more aberrant than other western populations.

For 5 populations of *C. baylyi*, prosomal lengths are a little less than 1 mm, with ♂ lengths ca 10% less than ♀ (Table 1).

Differential Diagnosis. *C. baylyi* is easily recognisable by the rounded projection on the middle inner surface of the second right exopodite segment (Re2) of the male (Fig. 1B,C). The only other species with a remotely similar structure is *C. australica*, in which the projection



FIG. 2. *Calamoecia baylyi* sp. nov. from WA; A, second and third segment of exopodite of ♀ fifth leg, specimen from Carnarvon basin (see Material for details); B, posterior aspects of ♂ right fifth leg, specimen from Carnarvon basin; C, posterior aspect of ♂ fifth legs, Cue population (after Bayly, 1984, fig. 4A); D, posterior aspect of ♂ fifth legs, Lake Grace population (after Bayly, 1984, fig. 5A). Scale bars = 0.1 mm.

is about a third along the inner edge and moreover sharp pointed.

Other notable features are variously shared with a limited range of other species. These include:

1) Outer edges of the exopods of the first pair of legs in both sexes have 3 spines each with a few large stout secondary spinules (Fig. 1A). Of other *Calamoecia* species examined for these spines, *C. halsei* has them and significantly *C. lucasi* s.s. does not (Bayly, 1998).

2) The claw of the right exopodite of the ♂ fifth leg (Re3), lacks an inner spine (Fig. 1B,C) as in *C. australica*, *C. canberra*, *C. halsei* and *C. zeidlereri* (Bayly, 1998). *C. lucasi* s.s. also lacks this spine but all other species have it (Bayly, 1992).

3) The left endopodite of the ♂ fifth leg (Ri1) is 1-segmented, very elongated, exceeding the length of the left exopod and bears 5 terminal and subterminal spines. This feature is shared with the same 4 species listed above, but usually not with *C. lucasi* s.s., which although of similar construction, has 2-5, usually 4 terminal/subterminal spines, (Bayly, 1961, 1992, 1998).

4) The left exopodite of the ♂ fifth leg is 1-segmented and with a spade-like terminal protrusion bearing denticles (Fig. 1B,C). In a

broad sense, this feature is shared only by *C. ampulla* and *C. lucasi* s.s., but the latter has no terminal denticles. In addition, *C. lucasi* lacks an inner subterminal spine that is present in *C. baylyi* and overall the length of the left exopodite is shorter relative to the left endopodite (a little greater than half in *C. lucasi* s.s. of three-quarters in *C. baylyi*).

5) On the ♀ fifth leg, the curved outgrowth on the inner distal corner of the middle exopodite segment (Re2) is relatively long in *C. baylyi* reaching about to the end of the distal exopodite segment plus its spines (Fig. 1D). In many other species, including *C. lucasi* s.s., this outgrowth terminates well short of the distal segment plus its spines (Bayly, 1961). Only *C. halsei* exhibits a similar condition (Bayly, 1998).

6) Again on the ♀ fifth legs, some of the 5 or 6 spines of the distal exopod segment (Re3) are only a little longer than the length of the segment in *C. baylyi* (Fig. 1D), as for *C. halsei* (5 spines) and *C. salina* also (but *C. salina* has only 2 terminal spines instead of 6). By contrast in most other species of *Calamoecia*, including *C. lucasi*, the spines are more than twice the length of the segment (Bayly, 1961) and significantly in *C. lucasi* s.s. there are only 5 spines, though some species have 6 (e.g. *C. trifida*). Only *C. zeidlereri* has shorter terminal spines (which number 5) (Bayly, 1984).

In the dichotomous key provided by Bayly (1992), *C. baylyi* would key out through couplets 1.2 8.9 and 11 to *C. lucasi*, but as pointed out above is easily distinguished from this species. Also, as shown by Bayly (1984) the Cue form of

TABLE 1. Prosomal lengths in mm of 10 ♂s and 10 ♀s from 5 populations of *C. baylyi*. * Only 6 ♂s and 4 ♀s measured.

Population	Mean length	Range of lengths	Mean length	Range of lengths	Source of data
CNP, Paroo	0.87	0.78 - 0.92	0.94	0.91 - 0.98	Original
Bloodwood, Paroo	0.89	0.85 - 0.94	0.96	0.92 - 1.01	Original
Carnarvon, WA*	0.89	0.86 - 0.90	0.98	0.97 - 1.00	Original
Cue, WA	0.86		0.96		Bayly, 1984
L. Grace, WA	0.93		1.00		Bayly, 1984

C. lucasi, i.e. now *C. baylyi*, is markedly larger than *C. lucasi s.s.*. The same applies in the Paroo where the 2 species are sympatric. In Lake Numalla (Currawinya National Park) which has a perennial population of *C. lucasi s.s.* a mean female prosomal length of 0.68mm has been recorded from measurement of 30 individuals (author unpublished) compared to 0.94mm (Table 1) of *C. baylyi* in a nearby claypan.

Ecology. *C. baylyi* lives in turbid temporary freshwaters, particularly in very turbid claypans (as in six sites in the Carnarvon region of WA (Halse et al., 2000), and the four present sites in the Paroo). In the Paroo it occurs in these pans soon after filling, passes through one generation and disappears after a few weeks (Fig. 3).

In the Carnarvon region it co-occurs with *C. canberra* or *B. triarticulata*, but not with the similarly sized *C. halsei* (female prosome length 0.81 – 1.00mm (Bayly, 1998)) which also lives in turbid claypans (S. Halse, pers. com.). Further work is needed to determine whether *C. baylyi* and *C. halsei* are competitors or have slightly different habitat preferences. The collection from near Lake Grace also had *B. opaquia* and *B. robusta maxima* (Bayly, 1984) while Halse's collections from the same locality contained just *B. robusta maxima* as well as *C. baylyi* (S.A. Halse, pers. comm.) In the Paroo other co-occurring copepods include *B. robusta robusta*, *B. triarticulata*, *B. timmsi*, *Calamoecia zeidler* and *C. canberra*, with co-occurrences of up to 4 species common (Hancock & Timms, unpubl. data). In all of these co-occurrences *C. baylyi* is a medium sized *Calamoecia*, larger than *C. canberra*, but smaller than *C. zeidler* and all the *Boeckella* species.

Distribution. *Calamoecia baylyi* occurs in the arid and semi-arid zone. In more detail, it is found widely in the western third of WA from Port Hedland in the north (Timms & Morton, 1988), through the Carnarvon basin (Maly et al., 1997), to Cue (Bayly, 1984) and near Lake Grace in the southwest (Bayly, 1984). It has not been detected in eastern WA, possibly through lack of habitat or collecting effort, nor in northern SA and southern NT which has been searched extensively by W. Zeidler (in Bayly, 1984). In the Paroo in northwest NSW and southwest Qld, which has been intensively studied by the author for 13 years, it occurs very spasmodically in time and space.

COMMENTS ON OTHER CALANOID COPEPODS OF THE PAROO

Boeckella fluvialis lives mainly in waterholes associated with the Paroo R, and occasionally in lakes (e.g. L. Numalla) and pans fed by Paroo floodwater, all in the Currawinya National Park (Timms, 1997a). It also occurs in waterholes in the lower Paroo area. In all the waterholes it was most common following major flows, reaching c. 5-12% of the total crustacean zooplankton. In Lake Numalla it was restricted to the Coomburra Waterhole that receives Paroo floodwater and soon disappeared when the lake returned to normal. In the 2 pans reached by floodwater it persisted for only 10 days despite the pans having water for many weeks. Though *B. fluvialis* lives in ponds and lakes elsewhere in its distribution (Shiel, 1986; Timms, 1989; Maly et al., 1997) in the Paroo it prefers riverine habitats.

Boeckella robusta robusta lives only in turbid claypans, but there are <10 records in the Paroo probably because it is short-lived and is not common when present (typically 1-3% of total crustacean zooplankton) (Fig. 3). Its presence in NW NSW and SW Qld (QM W25486) adds considerably to the 3 localities in NSW and Tasmania listed in Bayly (1964). Bayly's (1964) contention that the Tasmanian record was possibly a misidentification is supported by the lack of any records in a state-wide study of Tasmanian calanoid copepods (Walsh & Tyler, 1998). Furthermore the Sydney locality recorded by Sars (1896) probably has now been urbanised. Therefore the known distribution of *B. robusta robusta* should be modified to include only W NSW and SW Qld.

Boeckella timmsi also inhabits turbid claypans and has been collected even fewer times than *B. robusta*. It is known from only 2 claypans — the type locality in CNP (Bayly, 1998) and Turkey Pan at Bloodwood Station (Hancock & Timms, unpubl. data). In the latter it matured earlier and its existence was briefer than other copepods (Fig. 3). It may be more common and widespread, but its short life and early appearance in pans soon after filling when they are difficult to access means it is rarely collected.

Boeckella triarticulata occurs in almost all wetlands sampled in the Paroo, making it common and widespread, as it is in much of Australia (Bayly & Williams, 1973; Maly, 1984; Shiel, 1986; Maly et al., 1997). It even lives in hyposaline lakes to c.18 g/L. Overall it is most common in sites that are partly turbid and without

fish. Although not a characteristic species of turbid claypans (Timms & Boulton, unpubl. data), if they persist for many months, it maybe the only species present, and certainly the only species of *Boeckella* (Fig. 3) (Timms, in press).

C. canberra is also common and widespread throughout the Paroo, as might be expected from the distribution map given by Bayly (1984). It prefers turbid waters and is particularly common in claypans, even if they persist for months (Fig. 3). Though present in other lakes and river pools, it disappears in favour of *C. lucasi* when waters clear and does not survive should salinity increase above c. 5 g/L.

C. lucasi in the Paroo prefers larger lakes and riverine waterholes, often with less turbid water, e.g. L. Numalla, Corni Paroo Waterhole, L. Yantabadgee. Where fish are present it is usually the dominant calanoid copepod, as Maly & Maly (1997) have observed. It also occurs in smaller intermittent creek pools that persist for months, but not in turbid claypans, less persistent small pools or hyposaline lakes. These data concur with those on this species elsewhere in eastern and central Australia where it is widespread and common in larger permanent waterbodies (Bayly, 1978; Maly & Bayly, 1991).

C. ziedleri occurs throughout the Paroo, but only in turbid claypans, and then mainly in the early stages of filling. Its presence in the Paroo extends its distribution from NE SA (Bayly, 1984), and a collection from a claypan near Windorah, Qld (author, unpubl.) suggests it is distributed even further afield to include much of the central and eastern aridzone. Its presence in suitable intermittent waters, along with *C. baylyi*, *C. canberra* and occasionally *C. lucasi*, provide further exceptions to the observation that *Calamoecia* generally inhabits permanent waters (Bayly, 1978; Maly & Bayly, 1991).

Diaptomus lumholtzi occurs rarely in waterholes in the CNP, specifically Ourimpeere

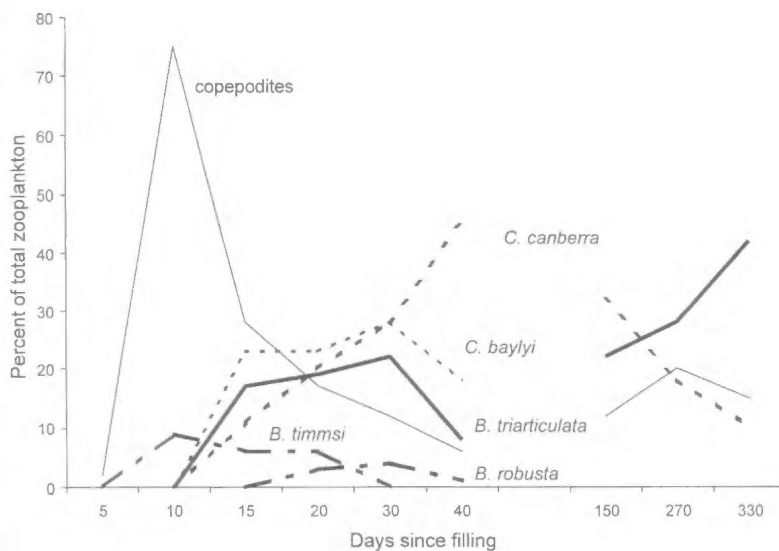


FIG. 3. Fluctuations in abundance of calanoid copepods in Turkey Pan, Bloodwood Station during a 'normal' fill in April-May 1998 and another prolonged fill in 2000 (mid to late stages only).

and Killanbirdie Waterholes 4 times over 13 years of observation. All records pertain to summer floods and numbers were always <0.1% of total crustacean zooplankton. These occurrences are well S of its normal distribution (Timms & Morton, 1988) and must be due to some individuals being washed down from the north and surviving for a limited period. Halse et al. (2000) also have found this species somewhat S of its known distribution across N Australia (Timms & Morton, 1988).

Gladioferens spinosus is even rarer in the Paroo, with just one record in the summer of 1995-6 from Ourimpeere Waterhole in CNP. This is the most northerly inland record for a species that normally occurs in some coastal freshwater lakes (Timms, 1973) and estuaries in SE Australia and N NZ (Maly & Bayly, 1991) and in floodplain rivers of the Murray-Darling Basin (Shiel, 1978; Shiel et al., 1982).

Co-occurrences are common among calanoids in the Paroo. The most numerous are between the larger *B. triarticulata* and the smaller *C. canberra* or *C. lucasi*, as noted elsewhere in inland Australia (e.g. Maly & Maly, 1997). Claypans regularly have multispecies complexes, with the relatively large *B. robusta*, then in decreasing order of size, *B. triarticulata*, occasionally *B. timmsi*, *C. ziedleri*, occasionally *C. baylyi*, and *C. canberri*. Bayly (1984) noted

that *C. ziedleri* co-occurs with either or both of *B. triarticulata* and *C. canberra*; they are well separated by size. Riverine waterholes also occasionally have many co-occurring species which may include any combination of *B. triarticulata*, *D. lumholtzi*, *G. spinosus*, *B. fluvialis*, *C. canberra* and *C. lucasi*. In both habitats up to 5 species and often 3-4 species, have been seen coexisting. Some are $<1.3\times$ other species in size and hence in possible competition (Hutchinson, 1951), but the situation is not persistent, as *B. timmsi* develops earlier than its congeners in pans, and other co-occurrences of similarly sized species (*B. triarticulata* / *D. lumholtzi* / *B. fluvialis* and *C. canberra* / *C. lucasi*) are linked with temporary disturbance by flood waters.

ACKNOWLEDGEMENTS

I thank Ian Bayly for encouragement in this project and Stuart Halse for making available specimens from Western Australia and for his comments on the manuscript.

LITERATURE CITED

- BAYLY, I.A.E. 1961. A revision of the inland water genus *Calamoecia* (Copepoda: Calanoida). Australian Journal of Marine and Freshwater Research 12: 54-91.
1964. A revision of the Australasian species of the freshwater genera *Boeckella* and *Hemiboeckella* (Copepoda: Calanoida). Australian Journal of Marine and Freshwater Research 15: 180-238.
1978. Variation in sexual dimorphism in nonmarine calanoid copepods and its ecological significance. Limnology and Oceanography 23: 1224-1228.
1984. A new species of *Calamoecia* (Copepoda: Calanoida) from South Australia, and comments on three congeners. Transactions of the Royal Society of South Australia 108: 147-154.
1992. The non-marine Centropagidae (Copepoda: Calanoida) of the world (Guides to the identification of the microinvertebrates of the continental waters of the world No. 2). (SPB Academic Publishing: The Hague).
1996. Inland-water calanoid copepods of Kangaroo, King and Flinders Islands: Biogeography and Ecology. Transactions of the Royal Society of South Australia 120: 1-6.
1998. New species of *Calamoecia* and *Boeckella* (freshwater Copepoda: Calanoida) from Western Australia and Queensland. Journal of the Royal Society of Western Australia 81: 177-182.
- BAYLY, I.A.E. & WILLIAMS, W.D., 1973. Inland waters and their ecology. (Longman: Melbourne).
- HALSE, S.A. & McRAE, J.M. 2001. *Calamoecia trilobata* n.sp. (Copepoda: Calanoida) from salt lakes in south-western Australia. Journal of the Royal Society of Western Australia 84: 5-11.
- HALSE, S.A., SHIEL, R.J., STOREY, A.W., EDWARD, D.H.D., LANSBURY, I., CALE, D.J. & HARVEY, M.S., 2000. Aquatic invertebrates and waterbirds of wetlands and rivers of the southern Carnarvon Basin, Western Australia. Records of the Western Australian Museum Supplement No. 61: 217-265.
- HALSE, S.A., R.J. SHIEL & WILLIAMS, W.D. 1998. Aquatic invertebrates of Lake Gregory, northwestern Australia, in relation to salinity and ionic composition. Hydrobiologia 381: 15-29.
- HUTCHINSON, G.E. 1951. Copepodology for the Ornithologist Ecology 32: 571-577.
- MALY, E.J. 1984. Dispersal ability and relative abundance of *Boeckella* and *Calamoecia* (Copepoda: Calanoida) in Australian and New Zealand waters. Oecologia (Berlin) 62: 173-181.
- MALY, E.J. & BAYLY, I.A.E. 1991. Factors influencing biogeographic patterns of Australasian centropagid copepods. Journal of Biogeography 18: 455-461.
- MALY, E.J. & MALY, M.P. 1997. Predation, competition, and co-occurrences of *Boeckella* and *Calamoecia* (Copepoda: Calanoida) in Western Australia. Hydrobiologia 354: 41-50.
- MALY, E.J., HALSE, S.A. & MALY, M.P. 1997. Distribution and incidence patterns of *Boeckella*, *Calamoecia* and *Hemiboeckella* (Copepoda: Calanoida) in Western Australia. Marine and Freshwater Research 48: 615-621.
- SHIEL, R.J. 1978. Zooplankton communities of the Murray-Darling System. Proceedings of the Royal Society of Victoria 90: 193-202.
1986. Zooplankton of the Murray-Darling system. In Davies, B.R. & Walker, K.F. (eds) The ecology of river systems. (Junk: Dordrecht).
- SHIEL, R.J., WALKER, K.F. & WILLIAMS, W.D. 1982. Plankton of the Lower Murray, South Australia. Australian Journal of Marine and Freshwater Research 33: 301-327.
- TIMMS, B.V. 1989. A study of the crustacean zooplankton of six floodplain waterbodies of the Lower Hunter Valley, NSW. Proceedings of the Linnean Society of NSW 110: 297-306.
1993. Saline lakes of the Paroo, inland New South Wales, Australia. Hydrobiologia 267: 269-89.
- 1997a. A Study of Wetlands of the Currawinya National Park. Unpubl. report to the Queensland Department of Environment, Toowoomba.
- 1997b. A comparison between saline and freshwater wetlands on Bloodwood Station, the Paroo, Australia, with special reference to their use by waterbirds. International Journal of Salt Lake Research 5: 287-313.
1998. A Study of Lake Wyara, an episodically filled saline lake in southwest Queensland, Australia. International Journal of Salt Lake Research 7: 113-32.

- In Press. Limnology of claypans of the Paroo, arid-zone Australia. *Verhandlungen Internationale Vereinigung Limnologie* 29.
- TIMMS, B.V. & MORTON, D.W. 1988. Crustacean zooplankton assemblages in freshwaters of tropical Australia. *Australian Journal of Marine and Freshwater Research* 21: 11-33.
- WALSH, R.G.J. & TYLER, P.A. 1998. Reconnaissance limnology of Tasmania IV. The distribution and ecological preferences of tasmanian species of freshwater calanoid copepods (Crustacea: Centropagidae). *Archiv für Hydrobiologie* 141: 403-420.

CONTENTS

BAEHR, B. & JOCQUÉ, R. Revisions of genera in the <i>Asteron</i> -complex (Araneae: Zodariidae): new genera <i>Pentasteron</i> , <i>Phenasteron</i> , <i>Leptasteron</i> and <i>Subasteron</i>	359
CANNON, L.R.G. & SEWELL, K.B. A review of <i>Temnosewellia</i> (Platyhelminthes) ectosymbionts of <i>Cherax</i> (Crustacea: Parastacidae) in Australia	385
COOK, A.G. & CAMILLERI, N. Additions to the rostroconch fauna of Australia and China	401
DALL, W. Australian species of Aristeidae and Benthescicymidae (Penaeoidea: Decapoda)	409
DAVIES, V.E. & LAMBKIN, C. A revision of <i>Procambridgea</i> Forster & Wilton, (Araneae: Amaurobioidea: Stiphidiidae)	443
DETTMANN, M.E. & CLIFFORD, H.T. The fossil record of <i>Elaeocarpus</i> L. fruits	461
EWART, A. Dusk chorusing behaviour in cicadas (Homoptera: Cicadidae) and a mole cricket, Brisbane, Queensland	499
FAUBEL, A. & CAMERON, B. Turbellaria from salt marshes of Coomera River, southeastern Queensland, Australia	511
FRITH, C.B. & FRITH, D.W. Bowerbird (Ptilonorhynchidae) biometrics, with observations on sexual dimorphism and intraspecific variation	521
GUILBERT, E. Western Pacific Tingidae (Heteroptera): new species and new records	543
HALLETT, S.L., ERSÉUS, C., O'DONOGHUE, P.J. & LESTER, R.J.G. Parasite fauna of Australian marine oligochaetes	555
HEALY, J.M., LAMPRELL, K. & KEYS, J.L. The 'water-trap' spiny oyster, <i>Spondylus varius</i> Sowerby, 1827 G.B. Sowerby I, 1827 (Mollusca: Bivalvia: Spondylidae) from Australia	577
KOFRON, C.P. & SMITH, R. Status of Estuarine Crocodiles in the populated coast of northeast Queensland	603

(continued inside cover)